

**ASPECTS OF THE GROWTH AND PHYSIOLOGY OF  
TROPICAL TREE SEEDLINGS IN SHADE**

By

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## ***DEDICATION***

**This thesis is dedicated to my parents, Mr. and Mrs. Rutahwaire.**



## ABSTRACT

Tropical forests are disappearing at alarming rates, and little is yet known about the ecophysiology of their species. One of the constraints of tropical forest management is the control of natural regeneration. Forest shade is known to be one of the most important factors influencing growth and development of seedlings at the forest floor.

The responses and adaptation strategies of light demanding and shade tolerating tropical tree seedlings to shade was investigated. Experiments have been performed in controlled environments in which shade conditions of tropical moist forests were simulated.

Plant responses <sup>that</sup> have been assessed are the relative growth rate, net assimilation rate and extension growth. Physiological parameters recorded include chlorophyll contents of leaves developed at low and high photon flux density; rates of CO<sub>2</sub> assimilation, respiration, and resistances to CO<sub>2</sub> transfer, under low or high photon flux density with low or high red/far-red ratio.

Whereas the shade tolerant *Khaya senegalensis* maintained a positive carbon balance at very low photon flux, the light demanding *Terminalia ivorensis* was below its light compensation point under the deepest shade, resulting in negative growth rates and assimilation rates. One of the most important findings has been the demonstration that many of the classic responses of trees to forest shade are brought about not through a reduction in photon flux density *per se* but through a shift in the spectral composition of the light. In particular, a reduction in the red:far-red which causes the expansion of leaf area to produce large thin leaves with a higher specific leaf area which are characteristic of shade grown material. This was found to be more pronounced in the light demanding *Terminalia ivorensis* than in the shade tolerant *Khaya senegalensis*.

When leaves raised under shade conditions are transferred to bright light, up to 50 % of the chlorophyll was lost, although in some



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species the photosynthetic system has great capacity to adapt.

It was also demonstrated that photosynthetic rates differ between light-demanding and shade-tolerating tropical tree species. All the light demanders showed capacity to adjust and switched from low to high photosynthetic rates when grown at low and high photon flux densities respectively. The shade tolerant *Khaya senegalensis* did not show this capacity: when grown at high photon flux density, its photosynthetic rate was low and did not differ from those of light demanding species when grown at low photon flux density. However, when the red/far-red ratio was low, *Khaya senegalensis* displayed slightly higher rates of photosynthesis than the light demanding *Terminalia ivorensis*.



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## CHAPTER ONE

### INTRODUCTION AND AIMS

According to Kramer and Kozlowski (1979) "basic physiological research can contribute to silvicultural and horticultural research and vice versa. The greatest overall progress will occur when physiologists learn more about how trees grow while foresters and horticulturalists learn more about physiology of trees, and these two groups co-operate to solve the problems of growing trees as efficiently as possible".

The physiological processes of a tree constitutes the machinery through which heredity and environment operate to control growth. Therefore, in order to understand why trees are affected by any particular factor or treatment, we need to learn how that factor or treatment affects their physiological processes.

This thesis concerns the response of tropical tree seedlings to shade. The subject is considered important to forestry in the tropics, both in natural forests and plantations. The extent of its importance can be judged only in relation to the present state of tropical moist forests. Thus, this introduction will serve briefly to review the general problem which for the last decade or so has concerned conservationists in many parts of the world.

#### 1.1 Extent and Distribution of Tropical Moist Forests (TMFs)

The world's tropical moist forests lie in a belt centred on the equator and extending 23° north and south to the Tropics of Cancer and Capricorn. They were estimated to occupy 935 million hectares (Sommer, 1976). Delegates to the Eighth World Forestry Congress (in Jakarta, 1978) were so disturbed at our lack of knowledge of the extent of the world's forest area that they asked the FAO to prepare an accurate report for the next congress in six years time (Grainger, 1980). FAO relies largely for its statistics on data supplied by individual governments, however such figures may be inaccurate and unreliable as shown by a recent example of the Philippines. In that country it was



claimed that forests covered 57% of the land area until satellite pictures (N.A.S.A.) gave the true figure as 38% (Grainger, 1980). Priority was given to obtain remote sensing data from LANDSAT satellites although their use could be limited by heavy cloud cover which is common over TMFs.

The FAO and United Nations Environmental Programme (UNEP) then carried out extensive surveys of forest ecosystems of Tropical America, Asia and Africa covering 76 countries in 1978. They used LANDSAT satellite images from the Global Environmental Monitoring System (GEMS). The data obtained were divided into four categories : closed tree formations, open formations, fallow or closed and open formations and shrub formations.

They showed that closed formations covered 1200 million hectares, 96.6% of which were broadleaved forests, 2.9% coniferous forests and 0.5% bamboo forests. 57% of the closed formation was in Tropical America, 25% in Tropical Asia and 18% in Tropical Africa (Steinlin, 1982); this is equivalent to 5.4, 2.7 and 1.9 million km<sup>2</sup> respectively (Caufield, 1982). These closed tree formations are found mainly in humid and semi-humid regions in the tropics and are the ones this chapter is about.

Tropical forests have been variously referred to as tropical high forests, tropical rain forests, equatorial rain forests and tropical moist forests (Richards 1952, Whitmore 1975, Longman and Jeník 1974, Poore 1976, Brünig 1977, Myres 1980, Steinlin 1982, and many others). In this study, they will be referred to as tropical moist forests (TMFs), which is a more descriptive term of the humid nature of the equatorial environment.

Tropical moist forests can be subdivided into equatorial rainforests and moist deciduous forests. Rainforests are wetter (4,000 - 10,000 mm of rain a year) than deciduous forests (1,000 - 4,000 mm). They have a larger number of tree species which do not shed their leaves annually, permanently moist soils, consistently higher mean annual air temperatures ( $\approx 30^{\circ}\text{C}$ ) and contain more diverse fauna and



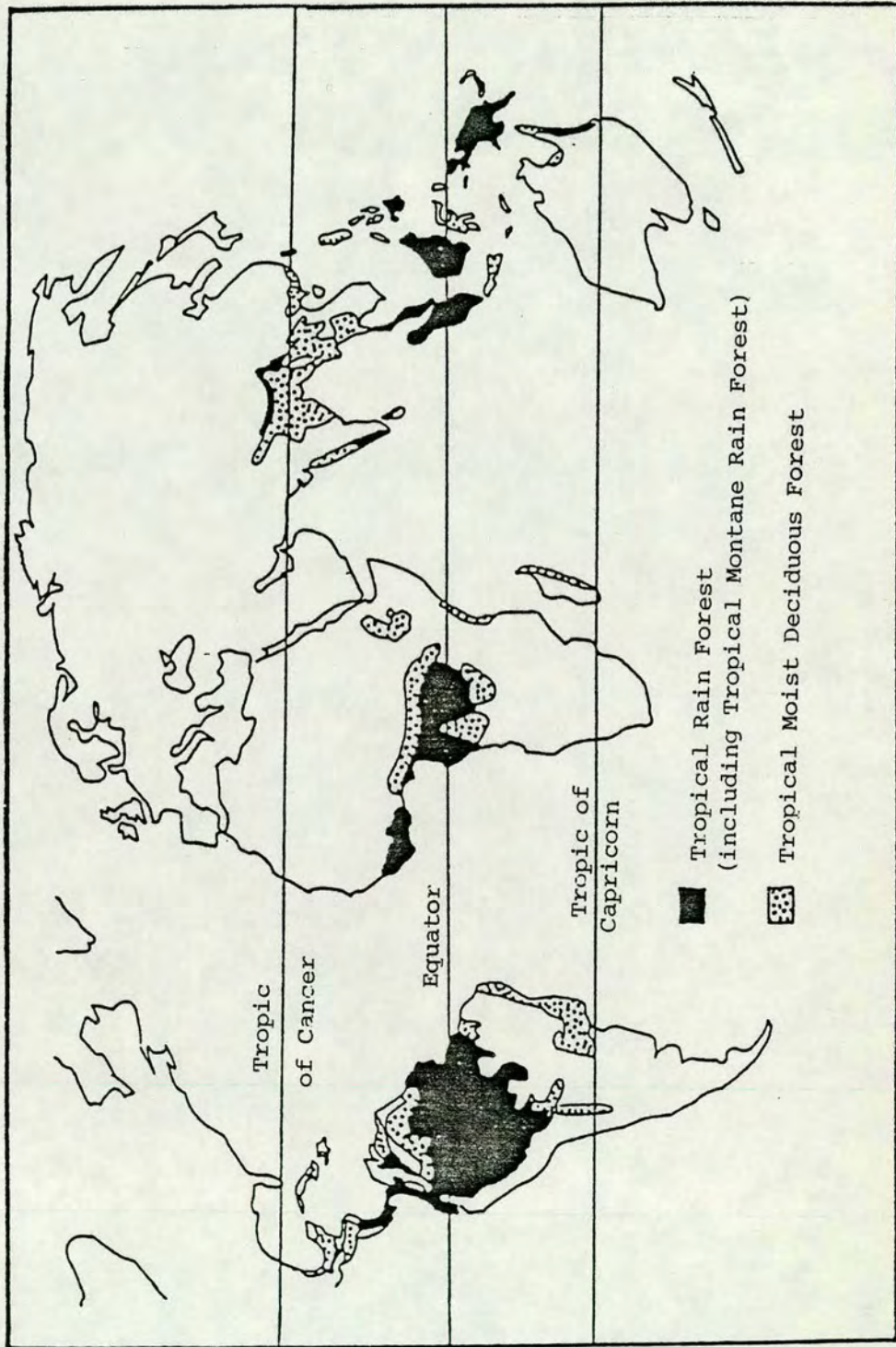


FIGURE 1: Sketch map of the world showing the distribution of Tropical Moist Forests. Modified after Poore and Allarby (1980).



flora. They extend into South America, Central America Isthmus, South East Asia; West, Central and East Africa (Figure 1).

Tropical moist forests cover only 7% of the earth's land surface and they contain 40-50% of all the species (Myres 1980). This area represents more than half of the world's forest area, and occupies 3% of the total earth's surface (Brünig 1977). These forests represent 60% of the world's forest growing stock and 69% the world's total forest productivity (Brünig 1977) and half of this area is closed formation.

Caufield (1982) presented TMFs in percentages by area in different zones of the world as follows :

<u>Area of Tropical moist forests (% of total)</u>	
Brazil	33 %
Zaire	10 %
Indonesia	10 %
Rest of latin America	25 %
Rest of South East Asia and Oceania	13 %
Rest of Africa	9 %

#### 1.1.1 Importance of Tropical moist forests

Tropical moist forests are probably the most complex and diverse terrestrial ecosystems known, and they contain the greatest concentration of species per unit area. Myres (1980) estimated that 40-50% of all plant species in the world are found in the tropics, whilst Evans (1982) considered this figure to be 85%. Estimates may vary, but there is a general consensus on species richness. This species richness of tropical flora has also been recently emphasized by Caufield (1982) who pointed out that on conservative figures, the TMFs contain two million species, less than 1% of which have been scientifically examined for their potential value to man (Levingston and Zamora, 1983). Even then, this wealth of identified species has in no sense been thoroughly investigated (Poore, 1976). The National Academy of Sciences (1975) pointed out that little is known even about tropical



plant species with promising economic value, and called for further scientific research.

In particular, TMFs are important because :

- 1) Certain parts of these tropical forests are the living area for indigenous people who derive all their means of subsistence from the forests e.g. The Pygmies of Ituri forest - Zaire.
- 2) They cover large catchment areas thereby regulating the quality and quantity of water leaving the catchment area. When removed, local hydrology is disturbed and soil may be eroded.
- 3) Species in TMFs have already made numerous contributions, through their genetic resources, to modern agriculture, medicine and industry.
- 4) In addition, they are habitats in which genotypes of plants and animals can perpetuate and express their evolutionary potential apart from serving as natural gene banks. In their virgin form, TMFs may be used in other scientific research areas such as standards against which changes in areas outside may be measured and evaluated: for instance they are known to have a moderating influence on climate, and consequently could be used as monitoring stations for measurement of regional and global changes such as atmospheric components of industrial pollutants.

The above benefits may be of a long term nature. The effects of total removal of substantial areas of these forests have been avenues of great speculation by scientists as summarized below :

- 1) The removal of forest cover is likely to have an influence on global climate through two main processes. The first of these is the transfer of carbon from biomass to  $\text{CO}_2$  in the atmosphere (Woodwell *et al.*, 1978). Enhancement of atmospheric  $\text{CO}_2$  concentration is certain to cause greater absorption of outgoing longwave radiation, but the extent to which this may lead to global warming is uncertain (Gribbin, 1979). The second process is the change in albedo consequent on the



vegetation removal, and its influence on local and global climate. On the carbon question, Lugo and Brown (1980) pointed out that as long as TMFs are managed for net yield or allowed to regenerate naturally, and provided that the clearfelled areas are a small fraction of the entire forested areas; the carbon balance will be maintained.

2) It is now generally agreed that the irreversible nature of complete destruction of TMFs is the loss of species and hence the gene bank (Gómez-Pompa *et al.*, 1972).

3) In general, the removal of any vegetation cover exposes soils to erosion (e.g. Spears, 1979). Natural forests show well developed mechanisms for efficient nutrient cycling stored in their biomass so that losses are minimal (Herrera *et al.*, 1981). Removal of these forests leads to leaching and laterization especially in the equatorial regions where annual rainfall totals are very high.

The points raised above (and many more uncovered) all suggest that destruction of forests especially the fragile TMFs has important socio-economic consequences (e.g. Poore, 1976) in addition to the effects on fauna and flora (e.g. Harrison, 1968). However, there seem to be conflicting views on what should be done. The conservationist lobby (e.g. Poore, 1976) suggests that these TMFs should be left alone since we know little about them. But can we afford to leave them alone ? It would be better to aim at (a) understanding the functioning of these forests (b) wise management of selected forests based on scientific principles (c) construction of alternative systems which serve additional needs, but at the same time avoid deficiencies of mindless exploitation. A combination of these three factors would resolve the conflict because TMFs are a resource that can be wisely exploited to serve the needs of millions of people in everyday life. Where wise use is lacking, then these forests are bound to be destroyed through various agents as follows.

## 1.2 The causes and extent of Tropical moist forest conversion

In spite of their importance (section 1.1.1) tropical moist forests



have continued to disappear at alarming rates (e.g. Spears 1979, Sommer 1976, and Myres 1980).

A distinction should be made between modification and transformation or conversion (of TMFs). Modification is essentially a process whereby the original structure, composition or dynamics of the forest is altered by human intervention or natural causes. This may be a result of extracting a few good trees or forest produce at a very small scale, or at the extreme, it can include forms of shifting cultivation which induce secondary succession in the forest. Provided that continuity is maintained with the original forest ecosystem and that there is no permanent loss of potential (e.g. soil degradation, extinction of species, etc....) the forest could return in a reasonable time to something like its original condition.

On the other hand, transformation or conversion is a completely different kind of change whereby the original or unmodified forest is totally removed and replaced by a man-made ecosystem or by inanimate structures e.g. plantations, roads, dams, towns, etc... (Poore 1976, Myres 1980, Grainger 1980 and Steinlin 1982).

### 1.2.1 Causes of conversion

The causes of tropical moist forest conversion derive from historical, socio-economic factors and lack of scientific knowledge of the species as well as poor management strategies.

#### 1) Historical:

Steinlin (1982) pointed out that, "What is historically significant is that areas that can support forest growth also offer the most favourable conditions for human life; and from the earliest time mankind and therefore socio-economic development has tended to concentrate in the forested regions of the earth. It is here that over centuries man has cleared large forest areas and converted them to other land uses and therefore made the greatest changes in the earth's vegetation. This process of conversion is still taking place but



it has shifted from the temperate zones of Asia, Europe and North America to the tropics and sub-tropics where population is now increasing rapidly. In some countries loss of forests has gone on steadily over two thousand years, in others it is a recent occurrence. But only in the last 150-200 years has net conversion of forests taken place in almost every country, and in recent years, the rate of disappearance has increased sharply".

## 2) Other factors:

In most cases, the contributing factors are peculiar to the socio-economic conditions. Most of the tropical moist forests are situated in Third World Countries often referred to as less developed countries (LDC) which are very poor by any standards and lack forestry awareness as well as being confronted with very high population growth rates: Caufield (1982) reported that rural population in these countries is expected to double within 27 years. The choice is not between feeding their people or retaining the forests for obvious biological productivity. Frequently, governments of these countries require foreign exchange earnings, and if these can be obtained immediately by forest exploitation, the long-term considerations have to be swept aside.

According to the World Bank report (1978), between 1900 and 1965 about half the forests in LDC were cleared for agriculture, intensive logging for veneer, sawn timber, chipwood and fuelwood. Taken together urban and industrial expansion take up to 12 million hectares of land each year (Evans, 1982).

### 1.2.2 Estimates of conversion rates

The rates of conversion vary from country to country. Though forecasts vary (Evans 1982, Steinlin 1982) it is estimated that in LDC forests are being converted at a rate of 15-20 million hectares per year (World Bank, 1978) and at present levels of demand, the remaining TMFs will disappear in a period variously estimated as between 60-80 years (Spears, 1979) to 312 years (Huguet, 1983) assuming a continuation



of the past rates of conversion. Myres (1980) estimated that the earth is losing around  $670 \text{ km}^2$  of TMFs a day, or an area the size of Wales a month. Lanly and Clement (1979) offered a more substantiated figure for total forest conversion, roughly 10 hectares per minute.

Myres (1980) reported a rate of  $245,000 \text{ km}^2$  per year. If this rate is sustained, the entire biome of some 9 million  $\text{km}^2$  will be eliminated within 37 years. The rate of conversion is likely to accelerate in many areas, and in hardly any area is it likely to decline. Indeed, certain areas are undergoing conversion rates fast enough to bring them to an end within a decade, whereas other areas could well remain little changed by the turn of the century. Examples of the more rapid rates of conversion include the Philippines, Peninsular Malaysia and most parts of West Africa which seem likely to be converted by 1990 at the least; little could remain of Central America's moist forests within 10 years. Extensive areas of Amazonia in Colombia and Peru could be claimed for cattle ranching (Myres, 1981) and various forms of cultivator settlements by the end of the century. By contrast, in Central Africa, meaning Gabon, Congo and Zaire with low human densities and abundant mineral resources, large expanses of little disturbed forests could well be retained by the end of the Century. Similarly, the western portion of Brazil's Amazonia, because of its remoteness and humid climate, may undergo moderate change. Myres (1980) reviewed the situation in 16 countries that comprise 70-75% of the biome and in 10 countries that contain the bulk of the richest types of TMFs. He pointed out that the main agents of conversion are the timber harvester, the forest farmer, the fuelwood gatherer and the cattle rancher. Altogether these agents are believed, "as a preliminary and approximate calculation" to be possibly accounting for the reported annual rate of TMF conversion. For more recent reviews, see Evans (1982).

### 1.3 Prescriptions for survival

In the previous section it was shown that while the estimates for rates of conversion may vary the agents of destruction are active and there is consistent alarm in all the regions. What is being done



about the situation ?

Poore (1976) warned that if great benefits are to be derived from the remaining tropical moist forests and undesirable consequences averted, certain precautions are necessary :

- 1) High standards of planning with appropriate legislation and caution in conversion from one land use to the other.
- 2) Good management and utilization based on sound scientific principles especially knowledge of the species.

The most obvious on-the-spot solutions are those concerned with increased research and development of tropical moist forest resources, increased education and public awareness about the importance of TMFs, development of alternative technologies to reduce demands of tropical forest products and land on which they stand, and an attack on the causes of the pressures upon these forests including poverty, unemployment, food and energy deficiencies and uncontrolled population growth.

Rubinoff (1982) opts for a more radical change and suggests :

- a) adoption of a new world-wide economic order,
- b) increased co-operation among nations to protect these valuable resources,
- c) rental of tropical forests by developed nations.

The convention of International Trade in Endangered species of wild fauna and flora opts for a ban. For instance, according to an article in New Scientist (11/8/83 p.411) "Mahogany" could be commercially extinct wood by 1990. Knees and Gardner (1983) suggest that trade in all mahoganies (about 23 species) should be controlled by the above convention. They reported that at present, only exporters of the Pacific coast mahogany (*Swietenia humilis*) need a permit. They also



TABLE 1

	Family	Genus
American Tropical-forest Region	Leguminosae	<i>Andira, Apuleia, Dalbergia,</i> <i>Hymenolobium, Mora</i>
	Sapotaceae	<i>Manilkara, Pradosia</i>
	Meliaceae	<i>Cedrela, Swietenia</i>
	Euphorbiaceae	<i>Hevea</i>
	Myristicaceae	<i>Virola</i>
	Moraceae	<i>Cecropia</i>
	Lecythidaceae	<i>Bertholletia</i>
African Tropical-forest Region	Verbenaceae	<i>Gmelina, Tectona</i>
	Leguminosae	<i>Albizzia, Brachystegia,</i> <i>Cynometra, Dialium,</i> <i>Erythrophleum, Gilbertio-</i> <i>dendron</i>
	Sterculiaceae	<i>Cola, Nesogordonia, Tarrietia,</i> <i>Triplochiton</i>
	Meliaceae	<i>Carapa, Entandrophragma,</i> <i>Khaya, Trichilia</i>
	Euphorbiaceae	<i>Drypetes, Macaranga,</i> <i>Ricinodendron, Uapaca</i>
	Moraceae	<i>Antiaris, Chlorophora,</i> <i>Ficus, Musanga</i>
	Sapotaceae	<i>Afrosersalisia, Chrysophyllum</i>
	Ulmaceae	<i>Celtis</i>
	Combretaceae	<i>Terminalia</i>
Indo-Malaysian Tropical-forest Region	Dipterocarpaceae	<i>Dipterocarpus, Dryobalanops,</i> <i>Hopea, Shorea, Parashorea</i>
	Moraceae	<i>Artocarpus, Ficus</i>
	Anacardiaceae	<i>Mangifera</i>
	Actinidiaceae	<i>Actinidia</i>
	Daphniphyllaceae	<i>Daphniphyllum</i>
	Dilleniaceae	<i>Dillenia</i>
	Gonystylaceae	<i>Gonystylus</i>
Australasian Tropical-forest Region	Myrtaceae	<i>Eucalyptus, Agonis, Baeckea,</i> <i>Backhousia, Osbornia</i>
	Dipterocarpaceae	<i>Dipterocarpus</i>
	Casuarinaceae	<i>Casuarina, Gymnostoma</i>
	Himantandraceae	<i>Galbulimima</i>
	Corynocarpaceae	<i>Corynocarpus</i>
	Dilleniaceae	<i>Hibbertia</i>
	Menispermaceae	<i>Carronia</i>
	Cunoniaceae	<i>Ceratopetalum</i>

Examples of families and genera containing dominant, abundant or endemic species of woody plants in the chief Tropical-forest Regions. Genera listed include those used in the present work and others referred to at various places in this thesis. Adapted from Longman and Jeník (1974).



suggest that all the other true mahoganies, those in the genera *Swietenia* from Central and South America and *Khaya* from West Africa should also be protected now as should unrelated tropical species with Mahogany-like wood such as Philippine mahogany (species of *Shorea* and *Parashorea*). This is because in the past decade, timber merchants have increasingly turned to Philippine mahogany, as supplies of true mahogany and other tropical hardwoods (see Table 1 ) have declined due to world-wide over-exploitation of TMFs.

In response to the great concern about TMFs destruction, there have been several other initiatives both by international agencies and more local institutions, towards instigating research on forest ecosystems and on important characteristics of constituent species. Three of these deserve mention.

#### 1. The Man and Biosphere (MAB) program

The Man and Biosphere (MAB) program of the United Nations has projects world-wide. One of its main objectives is testing approaches to scientific research and co-operation in environmental sciences. MAB also fosters interdisciplinary research and training on concrete problems of resource management. It seeks to provide scientific knowledge that can be used to solve the practical problems facing decision makers (Di Castri et al., 1981). Field projects at present in the tropics include:

a) The effect of human activities on nutrient cycling of TMFs of Amazonia: work began in Venezuela in 1974. The project revealed that human disturbances destroy the fragile nutrient cycling and lead to nutrient loss which compromise the rate of forest regeneration (Herrera et al., 1981).

b) In Indonesia, the MAB project has dealt with environmental effects on different kinds of land uses, entailing study of floristic, faunistic and soil changes in logged-over forests, secondary forests, dry-land farms as well as socio-economic conditions in the neighbouring settlements of transmigrants. The results showed that due to logging, residual trees were damaged, the soil was compacted which could lead



to low infiltration rates and soil erosion. Clear-felled primary forests were completely covered by 'pioneer' tree species within 6 months and these are low in economic value compared to primary forest species (Kartawinata *et al.*, 1981).

c) In Africa, the main objective of the Tai forest project in Ivory Coast is to improve scientific basis for management of TMF ecosystems. The results have shown that the needs of development are best served by planned, rational use of TMF resources (Dosso *et al.*, 1981).

## 2. Agro-forestry

Agro-forestry is a new term for an old concept (e.g. Taungya) of integrating agriculture with forestry. In recent years, research has intensified into this interaction, with the founding of the International Council for Research in Agro-forestry (ICRAF) in Nairobi, Kenya. This research is aimed at helping the rural economy and if successful it will make a major positive impact on everyday lives of millions of rural people (King, 1980). Also if shifting cultivation could be integrated into agro-forestry schemes in TMFs, by reducing the rate of destruction through stabilization of land use and intensification of production per unit of land without deterioration; this will relieve the pressure of TMFs (Bodowski, 1980).

## 3. The West African Hardwoods Improvement Project (WAHIP)

In the West African tropical moist forest, which was one of the world's major sources of tropical hardwoods, over a century of trade, mainly with Europe, has left its forests selectively felled. The rate at which these forests have been exploited is perhaps much greater than similar land which is converted to forest plantations. FAO in 1973 reported an increase from 1950-1973 in timber export from 4.2 to 53.3 million m<sup>3</sup> from West Africa alone. It is not surprising that 4% of the total closed forest area (6% of the total productive forest) in Africa is disappearing in West Africa alone (Steinlin, 1982); and that in Nigeria, with the highest population in Africa, there are prospects of having to import timber by the end of this decade (Myres, 1980).



Alternatively planting rates would have to increase by 300% (Spears, 1979) although Oseni (1980) reported only 1% of Nigeria's forest land to be under man-made forest cover.

Other countries have slowly responded to diminishing TMFs by establishing plantations of fast growing exotic species such as Pines and Eucalyptus, with indigenous species being rarely used (Grainger, 1980). The realization in 1970 that the quality and quantity of indigenous species had been seriously eroded, prompted a proposal by the Nigeria government to the United Kingdom Overseas Development Administration (ODA) for a collaborative scheme in research and development of indigenous hardwood species of West Africa. As a result WAHIP started at Forestry Research Institute of Nigeria in 1971, and later in 1974 a sister project was established in Scotland at the Institute of Terrestrial Ecology (ITE) at Bush near Edinburgh.

The joint aims of these two projects are to conserve and improve the remaining resources of these West African hardwoods in a long term programme of genetic-improvement, and a study of variation within species, using clonal stock. Extensive experimental plantings have been made at a number of sites, using material collections from other West African countries. At first, particular emphasis was on *Triplochiton scleroxylon* later, *Terminalia ivorensis* and *Terminalia superba*. A current screening trial of 20 species should soon indicate a suitable priority of other promising hardwoods (Howland and Bowen, 1977).

So sparse is our knowledge of tropical ecosystems and species that much useful work is possible on a more limited scale by individual investigators.

#### 1.4 The need to understand the response of seedlings to shade

1) At present, little is known about the ecology and functioning of TMFs (Persson 1974, Myres 1980) and even much less is known about tropical species of economic potential (National Academy of Sciences, 1975). Because of this lack of knowledge, it is still difficult to develop management techniques that can be applied successfully over



wider areas (Lugo *et al.*, 1981). Okali (1982) called for biological research into these tropical ecosystems for advancement of knowledge about the species concerned. He suggested field, or at least whole tree, physiological studies to be intensified in order to understand the factors controlling growth in TMF environment. For example, he pointed out that, "inability to interpret growth rings, and therefore to date many tropical trees remains a serious constraint to forest management as it limits the use of age in assessment of growth rates and hence productivity on which rational utilization depends".

2) Another major problem encountered in the management of these forests is the inadequacy of natural regeneration and the difficulty in controlling it. The most widely practiced method of obtaining natural regeneration is to open the forest canopy to allow sufficient light and warmth to stimulate regeneration by removing the overhead cover. However, control of natural regeneration demands a greater degree of scientific skill than mere felling.

The example of Budongo forest in Uganda is so clear that it may be mentioned in some detail. Eggeling (1947) stressed that, although the forests of Budongo had *Cynometra alexandri* [iron wood] suitable for railway sleepers; "it was for mahogany not iron wood that these forests were chiefly exploited". In an attempt to make Budongo a mahogany forest, his successors (Trenaman 1956, Dawkins 1958 and Phillips 1962) intensified the extermination of non-mahogany dominant species using contact arboricide and the axe in order to encourage natural regeneration of mahoganies as well as increasing their proportion in the forest. Analysis of this condemnation rather than commendation showed that the treatment resulted in a few mahoganies with still more "weed" species. Further analysis of this failure by Synnott (1975) revealed that the right canopy and conditions for planted seedlings were not being achieved; it then became necessary to reconsider the whole approach to regeneration and silviculture which was later confined to establishment of research plots.

3) This example and many others shows that we do not know enough about species requirements as far as the light climate is concerned.



Grouping of tree species as 'light demanders and shade tolerators' is much too simplistic to be useful. It is like grouping timber into "desirables (naturally durable) and non-desirables or weeds (perishable)", terms that were never precisely defined (Tisseverasinghe, 1981). Application of these terms in species utilization led to selective harvesting and erosion of the gene pool especially of mahoganies. Aluma (1979) attributed the concept of desirables and non-desirables to ignorance of other species and their timbers as well as lack of information about their properties. To this note, Tisseverasinghe (1981) stressed that full timber utilization based on knowledge of the species found in the forest, is the key to successful management as it gives more flexibility to silvicultural systems that will ensure natural regeneration and make other options attractive, "if as in temperate forests, nearly all the species were known and usable, the management systems would have been very different - they would have taken the whole forest into account instead of a few species".

4) Such knowledge is important not only in natural systems but in plantations too. Fast growing plantation species have been proposed in preference to natural regeneration based on economic grounds. However, Kio (1976) appraised the future of natural regeneration of TMFs with examples from Nigeria and Uganda. He examined comparative costs of artificial and natural regeneration. He then stressed that, "past econometric models have been manipulated to favour plantation systems due to adoption of false premises". In a detailed analysis, he showed that natural forests appear to be economically (and ecologically) superior to plantations. On the other hand, Catinot (1970) on reviewing the literature on enrichment planting, concluded that, "enrichment planting now has fewer and fewer supporters in the tropics : on the whole it has not given satisfactory results". On the contrary, as long as selective logging remains one of the causes of TMF conversion, Tisseverasinghe (1981) stressed that under certain favourable conditions, enrichment planting may be practiced in those over exploited forests. Plantation forestry is attractive economically and can show results in a short period; however, there are biological risks associated with fast growing plantation monocultures as discussed by Johnson, (1976).



Central to success of any of these methods is knowledge of species and their responses to certain variables such as light following forest disturbance. Looking ahead, knowledge of species responses is also important in any attempts to construct mathematical models to aid forest management.

5) According to Whitmore (1975) the "important part of the strategy of a species, enabling it to compete successfully with others in a TMF ecosystem, lies in its growth rate and response to light. This calls for studies of tree physiology to understand the adaptive strategies in the forest environment". First however, we must remove the tree or its propagules from its natural habitat and study it in isolation, more or less free from natural accidents to which it is otherwise subjected in a competitive environment. Only in such a simplified environment can complexities be unravelled.

### 1.5 Aims and Scope of this project

Central to an understanding of natural regeneration and succession is the response of seedlings to light, especially the development of leaf area and the nature of the carbon economy. It was realized long ago that species can be grouped into "Light demanders and shade tolerators", but only relatively recently has it been possible to make good measurements of relevant physiological parameters which give rise to such differences in behaviour (e.g. work on sun and shade ecotypes by Björkman and Holmgren, 1963).

According to Whitmore (1975):

"We remain in almost complete ignorance of the basic differences between shade tolerating and light demanding tropical tree species. This remains largely an unexplored field of inquiry, ripe for investigation by methods which are well established".

As will be shown later in Chapter Two, the seedlings on the forest floor are faced with shade-light of which much of the



wavelengths useful for photosynthesis have been filtered out by successive layers of foliage. Two questions do arise :

1) Do species under these conditions differ in their efficiency in utilizing this light ?

2) Growth implies that net photosynthesis exceeds respiration, so that there is net gain of carbon fixed by the plant: do species differ substantially in their carbon economy ?

To answer these questions, studies of plant response to shade must take into account the spectral changes that characterise the forest shade, especially the red:far-red ratio (R/FR). There are numerous reports that shade produced by neutral filters influences the growth and development of plants. However, these filters may not have been neutral in their spectral properties especially in the far-red part of the spectrum, and their spectral properties may not have been adequately recorded. One of the requirements of this project is thus to clarify this issue by differentiating between the responses to a reduction in photon flux density *per se* compared with a reduction in R/FR ratio.

In relation to regeneration of TMFs, it is important to investigate species differences. Many of the species prized for their timber (e.g. *Khaya senegalensis*, African mahogany) are climax species which grow slowly from large seeds and produce dense wood: They are also shade tolerators. Other, fast growing, species like *Triplochiton scleroxylon*, *Terminalia ivorensis* and *Terminalia superba* are also useful for timber production and they are known to be light demanders. Management of natural TMFs or plantations for production of these species requires an appreciation of their basic differences in response to shade, especially at establishment.

Specifically, the work presented in this thesis has the following aims :

1) Characterisation of seedling growth in relation to shade, using



contrasting species and employing techniques of growth analysis.

2) Characterisation of the carbon economy of these seedlings by investigating the rates of photosynthesis and respiration. This will require investigations of leaf area, chlorophyll levels, and the analysis of diffusion pathways including the stomatal component.

3) Identification of the separate roles of (i) reduced photon flux *per se*, and (ii) reduced R/FR in influencing the development of photosynthetic capacity.

As far as the range of species to be investigated is concerned, it was realized at the outset that much would depend on the availability of viable seeds. However, the intention was to choose examples of light demanders and shade toleraters which also happen to be important timber sources. In addition, in order to cover the full range of possible biomass-producing systems, it was decided to carry out some comparison between the trees and the giant sedge, *Cyperus papyrus*: it is a good experimental material and a very important species in Uganda, it also contrasts well with the tree species.



## **CHAPTER TWO**

### **THE LIGHT CLIMATE IN THE REGENERATION ZONE**

Past and present field investigations suggest that light is the primary limiting environmental factor for carbon gain and growth of seedlings and saplings in the understory of TMFs (the regeneration zone). It is known also that the amount and quality of this light is influenced by the structure of the canopy.

#### **2.1 Structure of the closed TMF canopy**

To understand the processes that go on inside a TMF canopy, it is important to mention briefly its structure. The structure common to all climax TMFs is manifested in the stratification of trees, shrubs, vines and herbs. Terms like layer, storey and canopy have all been used to describe the form of the crowns of tropical forest trees. Whereas the temperate forests are usually two tree strata or even one, TMFs may have several, usually more than three, although this may not be so obvious (Brown, 1919).

The complex structure of TMFs has been described in detail (e.g. Richards 1952, Baur 1964). Richards (1952) recognised that tree strata in a mature TMF, though always present, are ill defined and are seldom easy to recognise by casual observations. However, he pointed out that trees of intermediate heights are present and that the mixture of species is so great that these hypothetical height intervals never really exist as stories. Thus, Richards (1952) defined a stratum or a storey as a layer of trees whose crowns vary in height about a mean; and in a several-layered forest community, each stratum will have a distinctive floristic composition. But, since the forest is dynamic continually growing and regenerating, a proportion, perhaps the majority of individual trees in the lower stories, will eventually belong to species which will reach a higher stratum of dominants and co-dominants when mature.

Profile diagrams of a section of a forest have been drawn by many research authors to illustrate structure and composition (e.g.



Eggeling 1947, for Budongo forest in Uganda; Jones 1948, Keay 1949, Richards 1952, Jones 1955, in Nigeria; Fox (1968) for Gola forest reserve in Sierra-Leone; and Kato et al., (1978) for Pasoh forest in Malaysia). From these and many other profile diagrams, there seem to be three or more layers. Richards (1952) pointed out that the basis of these layers depends on autotrophic plants which depend directly on light for their existence and can be divided into two groups according to the method of reaching this light: the mechanically independent or self-supporting that reach the light without assistance from other plants (trees, shrubs and herbs), and the mechanically dependent plants (climbers, stranglers, epiphytes and semi-parasitic epiphytes). In this section, we are concerned basically with the layering of mechanically independent plants. These layers have often been designated A to E downwards. Thus:

A) May be continuous, but more often composed of scattered and isolated emergent trees that outgrow their associates. These species are relatively shade intolerant (e.g. Smith, 1962); spending much of their life in full sunlight. The most valuable timber species such as the famous Honduran Mahogany and Spanish Cedar of Central America are usually emergents (see Table 1).

B) If stratum A is discontinuous, stratum B forms the main upper canopy of the forest and often contains the most heterogenous mixture of species, receiving full sunlight from above, but very little from the sides.

C) This is the subordinate stratum composed of the most shade tolerant species. These receive little or no direct sunlight from above and none from the sides, and are composed of overtopped or suppressed trees (Smith, 1962).

D) A shrub and herb layer, close to the forest floor, with tree seedlings and saplings.

E) The forest floor, popularly known as the dim layer (Longman and Jeník, 1974). It contains the seed bank and is the germination and



establishment zone.

The primary interest of this work focuses on processes that control the growth of tree seedlings in the dim layer (Stratum E) or in openings. At this point it is necessary to consider possible sources of light reaching such plants.

## 2.2 Gaps in the Canopy

Natural forests throughout the world are fundamentally similar in their patterns in space and time because the same processes of succession and maintenance operate (Whitmore, 1982). These patterns and processes of change in a forest are expressed by a growth cycle in which three arbitrary phases can be distinguished: gap, building and mature. These structural phases are always altering as one phase changes to the next. Their coarseness depends on what creates the gaps.

In virgin forests, gaps or forest openings are created by the falling down of dead trees and the loss of parts of larger individuals in the A and B stratum. Natural decay by fungi, destruction by insects or mammals and windthrows by hurricanes are the usual factors causing such openings (e.g. Longman and Jeník 1974, Lugo *et al.*, 1981, Whitmore 1982). These gaps are heterogenous in nature and they vary from a few metres to several kilometres across.

When in a closed forest a tree dies or falls a gap forms. Such gaps play a very important role in the processes of natural regeneration on the forest floor. However, when large and apparently still vigorous trees are overthrown by a tornado or other extreme wind (e.g. Hurricane David of 1979 in Dominica, Lugo *et al.*, 1981), the gap may then be larger. In undisturbed forests, naturally formed gaps are numerous, and the remains of trees are seen everywhere, though owing to rapid rate of decay they disintegrate more quickly than in temperate forests (Richards, 1952). A natural gap is thus a scene of a secondary succession on a very small scale.



When a tree or groups of trees grow up to fill the gap, this process is called gap-phase replacement (Watt, 1947). The floristic composition depends on gap size, with light demanding species occurring where gaps are large and the structural mosaic is coarse, and shade-toleraters where gaps are small and the mosaic fine. Floristic fluctuation occurs where small gaps alternate in time with large ones. Thus, gap-forming processes drive the forest growth cycle and determine forest floristics. To the extent that gaps develop unpredictably there is an element of randomness in forest composition (Whitmore, 1982).

The microclimate of these forest openings thus plays an important role in stand management and regeneration (Richards 1952, Smith 1962, Lee 1978). The changes from a forest climate to that of an open area are most abrupt in the transition zone or forest edge but, except in very large gaps, the forest influence is detectable throughout the opening. According to Lee (1978) differences in microclimate with distance from the forest edge are of particular interest; the gradation of conditions is intimately associated with the relative size of the cleared area and its geometrical configuration. In a large clearing on level land, the potential period of direct-beam radiation at the forest edge depends on the angle of exposure (orientation of that angle and, to a less extent, latitude).

So far, it has been noted that the environment above and below the canopy differs between large and small gaps. Conditions in a large gap are more like those outside the forest whilst in a small gap more like the forest interior.

### 2.3 Microclimate under the canopy

A dense forest canopy drastically modifies climate near the ground. The following are some of the effects as given by Lee (1978);

- 1) Net all-wave radiation measured near the ground is usually less than that above the canopy by at least an order of magnitude during clear days. This difference is less at night.



2) Wind speed is modified less severely; under a closed canopy it may be only 20% of that observed above the forest, but in more open forest types it is greater than 50%.

3) The relative amount of precipitation that reaches the forest floor varies with both the interception (storage) capacity of the canopy and the intensity and duration of precipitation. On average, rainfall deficits under mature hardwood canopies may vary from less than 10% during the leafless period to more than 20% during the growing season; the average deficits are usually greater under coniferous types especially during the dormant season.

4) During the periods when net all-wave radiation is positive, air temperatures near the forest floor are less than those at the top of the canopy; at night when net radiation is zero or negative, air near the forest floor is slightly warmer than it is above the canopy.

5) Relative humidity (R.H.) near the ground exceeds that above the canopy during the day primarily because of the temperature differences; at night with virtually isothermal conditions, higher relative humidities occur near the forest floor because the ambient vapour pressure is slightly greater at that level.

All these factors are likely to influence regeneration and the growth of seedlings at the forest floor. However, it is generally held that the light climate exerts an over-riding effect.

#### 2.4 Light levels at the forest floor

The amount of light reaching the forest floor depends on the density of vegetation foliage through which it passes. To facilitate description of the amount of light that reaches the floor of a plant community, Weisner (1907) introduced the notation of "relative irradiance" expressed as the average percentage of the external light.

Although the methods and equipments used by early workers to measure relative irradiance varied a lot and were not very accurate,



there was a general similarity in the values that were measured and reported for the forest floor.

Weisner (1895) in Java, using an actinometer, reported values of less than 1%. This value was also reported by McLean (1919) in the forests of South Brazil. Allee (1926) at Barro Colorado Island in Panama reported values of  $\approx 3\%$  for dense shade. Carter (1934) in Mora forest of Guyana, Brünig (1947) in Indonesia tropical moist forests and Cachan (1963) in South Ivory Coast tropical moist forests reported similar values to those of Weisner.

In different tropical moist forests, Evans (1956) in Nigeria, Whitmore and Wong (1959) in Singapore and Schulz (1960) in Surinam reported values between 2 - 5% as did Björkman and Ludlow (1972) in the sub-tropical forests of Southern Queensland, Australia.

Synnott (1975) using a specially constructed spectroradiometer reported for Budongo forest floor in Uganda, total irradiance of  $\approx 3\%$ . More reviews on this subject are given by Richards (1952) and Whitmore (1975).

Furthermore, Longman and Jeník (1974) reported that relative irradiance decreases according to the density of foliage down to approximately 25% in the middle and lower layer trees. It then drops to about 3% or lower in the dim layer, where values of under 1% have been repeatedly measured.

In other stands of vegetation, Larcher (1980) reviewed work on boreal birch-spruce mixed forest, and Pine forests. Only 2% of the incident short-wave radiation reaches the floor of both forests.

From these reviews, it is clear that the forest floor receives little quantity of light or photosynthetically active radiation (PAR). Probably the lower limit for existence of vascular plants lies not far below the range encountered in the dim-layer.

To understand how plants under the influence of very low PAR



grow, it is also important to characterise this light by its spectral distribution as it reaches the forest floor after successive screening effects by various foliage layers.

## 2.5 Vegetational shadelight

This is the light encountered within or beneath a vegetation canopy. It has two main components:

- (1) Unfiltered daylight (direct sunlight, diffuse skylight or diffuse light from the clouds) which has passed through holes in the canopy.
- (2) Filtered or attenuated daylight, the spectrum of which has been altered by the canopy through the process of absorption, reflection and transmission.

This subject has recently been reviewed by Morgan and Smith (1981) and the most important aspect of shadelight is that it affects growth and development of plants found beneath the canopy where both quantity and quality of light have been altered. Climatic conditions have only a small effect on the spectrum of vegetational shadelight whilst vegetation structure and density have large effects (Morgan and Smith, 1981).

Leaf canopies do not simply transmit light, but as is common with all other biological surfaces, leaves reflect short-wave radiation. The proportion of incident light reflected depends upon several parameters such as leaf angle (de Wit 1965, Duncan *et al.*, 1967), leaf and cuticle thickness. Light passing through a leaf is not simply reduced in flux density, but also radically altered in terms of spectral quality, due to the action of various leaf pigments. The short-wave spectra for reflection and transmission of green leaves are largely a consequence of absorption by chlorophylls (Woolley, 1971).

Typical leaves transmit a small proportion of incident light in the green band around 550 nm (1-20%) but are otherwise effectively opaque in the visible range (400-700 nm). A dramatic change from opacity to



near transparency occurs about 700 nm, so that transmitted light has a very high far-red proportion. Detailed analyses of spectral energy distribution under leaf canopies are given by Holmes and Smith (1977).

At this stage, it is necessary to consider the light which has passed through holes of the canopy and its contribution to the processes of growth and development of tree seedlings at the forest floor.

### 2.5.1 Sunflecks

Sunflecks are a special case of vegetational shadelight in which direct sunlight breaks through a hole in the canopy. They are composed of direct sunlight, sunlight reflected from vegetation, diffuse skylight and vegetation-filtered diffuse skylight (Morgan and Smith, 1981). Published spectra show that in the centre of all sunflecks, direct sunlight predominates (Yocum *et al.*, 1964; Vezina and Boulter 1966; Holmes and Smith 1977b). These patches of light caused by direct solar beam passing through the canopy gaps move in arcs as the sun changes position, the flux density being equal to or less than that of the direct solar beam in the open, depending on the proportion of the solar disk visible at that location.

Tasker (1977) reported that the spectrum can vary considerably across a sunfleck, and at the periphery, the red to far-red (R/FR) ratio may be lower than in the ambient shade. With increasing gap size the spectral distribution tends towards that of daylight from a clear sky. Hence, a rapidly fluctuating light regime may occur. Photosynthetically active radiation (PAR) might vary over two orders of magnitude within a few minutes, and therefore photosystems require to be capable of harvesting very low flux densities of photons, but at the same time tolerate the high fluxes of sunflecks without photodestruction occurring. Woodward (1981) stressed that such high photon flux densities cause sudden variations in leaf temperature, leading to water stress.

Several workers in TMFs have estimated the contribution of



sunflecks. This also means that the measurement of PAR must take account of such variability; Björkman and Ludlow (1972) showed that comparisons of total irradiance inside and outside the forest over-estimate the amount of PAR on the forest floor, 3 to 15 fold. However, the importance of this depletion is reduced by the large proportion of light reaching the ground in sunflecks. Light in sunflecks was calculated as 40% and 60% of the day's total at the forest floor in two plots in Singapore, and 70% in Nigeria by Whitmore and Wong (1959) and Evans *et al.*, (1960) respectively. In Queensland, Björkman and Ludlow (1972) showed that sunflecks contributed 10.5% of the energy between 300 and 2400 nm and 61% of the quanta between 400 and 700 nm reaching a plant on the forest floor whilst Synnott (1975) in Budongo forest estimated them to be at least 35-40% of total radiation.

Recently, the light environment in the understory of a Hawaiian evergreen subtropical forest, was characterized using photosynthetic photon flux density sensors, and hemispherical "fish eye" photographs of the canopy (Pearcy 1983). He estimated that 40% of the total daily PAR reached the forest floor and was contributed by sunflecks. The understorey received 2.4% of the light reaching the top of the canopy. Nearly all the sunflecks had peak photon flux densities greater than  $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ , but two-thirds were less than 0.5 minutes in duration. The number of minutes of sunflecks received per day at any site was highly variable depending on cloudiness and the overstory canopy structure. Growth of understory saplings studied was highly correlated with estimates of minutes of sunflecks.

Other work reported earlier (e.g. Evans 1956; Evans *et al.*, 1960) provided only relative estimates of canopy transmission and were based on techniques that do not allow for determination of photosynthetically active radiation. The only study in which the photon flux density (PFD) available to plants in the understory of a tropical forest was measured (Björkman and Ludlow, 1972) showed that sunflecks were a major fraction of the available PFD and were responsible for a sizeable portion of daily  $\text{CO}_2$  uptake by the forest floor plants.



Pearcy (1983) reported measured values of PFD in the shade under the canopy of Pahore Gulch forest (Hawaii) as ranging from 10-30  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , but short duration sunflecks were relatively frequent. However, because of the complex kinetics, it is still difficult to determine the quantity of photons received during sunflecks of different length; but longer sunflecks certainly contribute a substantial fraction of the total PAR.

### 2.5.2 Spectral distribution

A striking aspect of spectral irradiance within the depth in a plant canopy is that occurring in the red and near infra-red parts of the spectrum (Ross, 1975). In all vegetational shadelight spectra, there are large differences in attenuation between the far-red and the visible radiation (Morgan and Smith, 1981). At the bottom of a dense canopy, spectral changes are greatest (McCree, 1981).

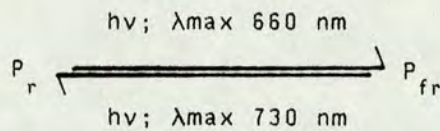
Evans (1939) by means of a Weston cell and filters estimated the composition of the undergrowth light in a forest in Nigeria. He showed that there was a considerable increase in transmission of the forest canopy just beyond the red end of the visible spectrum. Richards (1952) pointed out that the light near the infra-red cannot possibly be used in photosynthesis since it is outside the range of absorption of chlorophylls. Whitmore (1965) in a study of light conditions in Ecuador, reported on the filtering effects on the light penetrating the ground vegetation, and remarked that this was likely to include a bigger fraction which has been reflected from or transmitted through the green plant leaves. This component is known to be rich in green, far-red and near infra-red wavelengths. Longman and Jeník (1974) noted that the screening and filtering effects of the tropical moist forest canopy must alter the spectral composition of the non-sunfleck light reaching the lower layers, which meant that relatively higher proportions of far-red and infra-red were transmitted through the canopy. Larcher (1980) stressed that beneath a canopy of leaves, a green shade prevails, and in the depth of a forest, only far-red and infra-red light remains.



The degree of shading by leaves may be described numerically by calculating the ratio of photon fluence rates in 10 nm band widths centered at 660 nm and 730 nm as has been measured by Sinclair and Lemon (1973); Holmes and Smith (1977b). These wavelength are important because they are the action maxima for the photoreceptor phytochrome (Morgan and Smith, 1981) and this affects photomorphogenesis. Their ratio is usually denoted by symbol  $\zeta$  (zeta), the ratio of photon flux density between 655 nm and 665 nm (red light) to that between 725 nm and 735 nm (far-red light):

$$\zeta \text{ (zeta)} = \frac{\text{Photon flux density (655-665 nm)}}{\text{Photon flux density (725-735nm)}}$$

The property which allows phytochrome to act as a light quality perceptor is its photochromicity, that is the capacity of phytochrome to exist in two photoconvertible, isomeric forms (Smith, 1981) according to the wavelength ( $\lambda$ ) of the photons ( $h\nu$ ). Thus :



$P_r$  and  $P_{fr}$  are phytochrome proportions in the red and far-red, they are relatively stable and the photoconversions pass through different, highly unstable, intermediate states in the two directions. According to Smith (1981) the absorption spectra of  $P_r$  and  $P_{fr}$  overlap below  $\approx 730$  nm, simultaneous photoconversion in both directions sometimes known as "cycling" occurs with broadband visible irradiation. At 'natural' photon flux densities, photoequilibrium is rapidly achieved, and the proportions of  $P_r$  and  $P_{fr}$  present at equilibrium are determined by the spectral photon distribution of the radiation. According to Smith (1973), "Since the extinction coefficients of  $P_r$  and  $P_{fr}$  are highest in the red ( $\max \lambda \approx 660$  nm) and far-red ( $\lambda_{\max} \approx 730$  nm) wavebands, respectively, the proportions of  $P_r$  and  $P_{fr}$  present at equilibrium may be seen to reflect principally the relative amounts of red and far-red wavelength ( $h\nu$ ) in the incident radiation". Smith



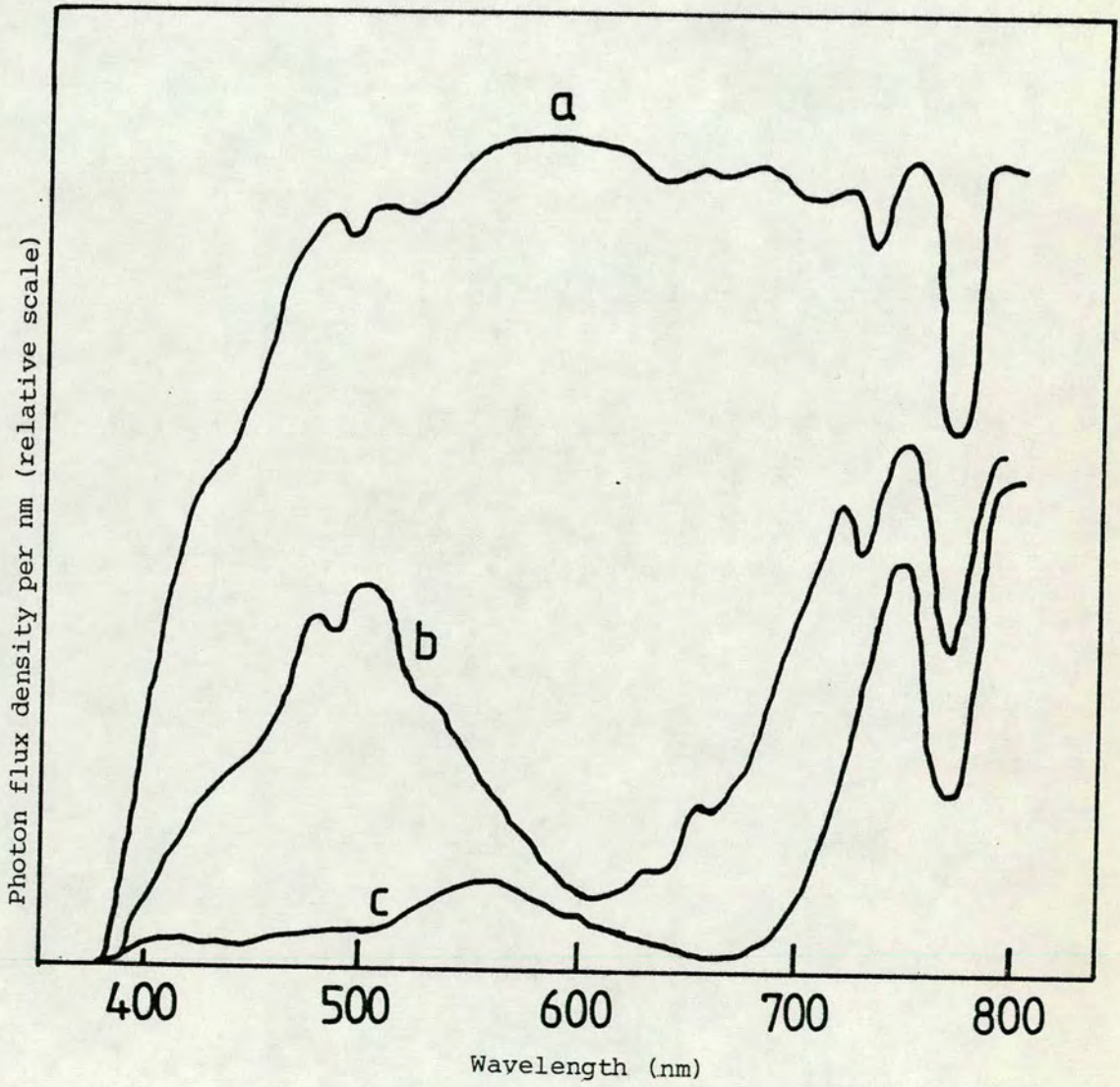


FIGURE 2: Spectral photon fluence rate of natural global radiation under various terrestrial conditions (redrawn from Smith, 1981).

- (a) Mid-day, clear skies
- (b) Sunset, clear skies
- (c) Under a vegetation canopy



(1973) presented the hypothesis that phytochrome acts as a perceptor of light quality in the red and far-red spectral regions. For the purpose of this study, a more descriptive abbreviation of zeta (R/FR) will be used.

A recent and detailed account of the spectral properties of shade is one contained in papers by Smith (1981). He showed that on the shaded side of a hedgerow or a stand of vegetation there is a substantial drop in the R/FR ratio (Figure 2). Using specially constructed light quality cabinets he was able to demonstrate that R/FR ratios can be reduced experimentally to those found in natural plant communities. He obtained values ranging from 3.0 to approximately 0.2, covering most of the range found in nature.

The characterization of shade by its R/FR ratio has stimulated much interest in recent years. Spence *et al.*, (1971) calculated the values of R/FR for sunlight as 1.3 whilst Smith (1981) gave this value as approximately 1.2.

Stoutjesdijk (1972) found no difference in R/FR ratio of the forest floor between the TMF he studied and various woodland types in the Netherlands. He concluded that under all canopy types, the values of R/FR ratio were low in a range of 0.2 to 0.4, compared to the much higher values for full sunlight.

Most work has been done under temperate tree canopies and herbaceous plants as well as agricultural crops. Limited work has been reported for tropical moist canopies. In this study it has been assumed that the lower values of R/FR ratio reported for other tree canopies may be used to approximate those under TMF canopies.

Morgan and Smith (1981) have summarized R/FR ratios for closed vegetational canopies and spectral variations as reported in the literature (Table 2).

In this literature review, it has been shown that the possible sources of light for plants on the forest floor are sunflecks that pass



TABLE 2

	CANOPY	SKY CONDITION	R/FR	REFERENCES
(a)	Crops			
	Wheat	Clear	0.49	Holmes and Smith (1977b)
		Overcast	0.59	Holmes and Smith (1977b)
	Maize	Clear	0.20	Yocum <i>et al</i> (1964)
(b)	Sugarbeet	Partially overcast	0.11-0.41	Holmes and Smith (1975)
	Tea	Overcast	0.09-0.15	Hadfield (1974)
	Broadleaved deciduous woodland			
	Beech	All conditions	0.16-0.64	Tasker and Smith (1977)
(c)	Oak	Clear	0.12-0.17	Federer and Tanner (1966)
	Sweet Chestnut	Clear	0.12	Coombe (1957)
	Sugar maple	Clear	0.14-0.28	Vezina and Boulter (1966)
		Clear	0.08-0.11	Federer and Tanner (1966)
(d)	Coniferous Evergreen woodland			
	Spruce	Clear	0.15	Federer and Tanner (1966)
		Overcast	0.46	Federer and Tanner (1966)
	Red pine	Clear	0.33	Federer and Tanner (1966)
(e)	White pine	Clear	0.25-0.26	Federer and Tanner (1966)
	Jack pine	Clear	0.32	Federer and Tanner (1966)
	Tropical moist forest			
	Montane	Bright	0.22-0.30	Stoutjesdijk (1972b)
(f)	Lowland	Overcast	0.77	Stoutjesdijk (1972b)
		?	0.26	Stoutjesdijk (1972b)

R/FR for Shadelight beneath various vegetational canopies (adapted from Morgan and Smith, 1981a).



through the gaps in the canopy. Also the light climate at the forest floor is influenced by the canopy foliage resulting in changes in spectral properties especially the R/FR ratio. In the next chapter, evidence will be presented as to how the plants respond to shade, i.e. reduced photon flux density *per se* and reduced red/far-red ratio.



## CHAPTER THREE

### RESPONSE TO SHADE

There are several distinct types of plant reaction to shade. In brief, these reactions are :

- 1) The relationship between the rate of photosynthesis and photon flux density (PFD) is generally different for leaves that have developed in shade versus sun. Shade leaves display higher rates of photosynthesis at low photon flux densities.
- 2) Leaves developed in shade are frequently thinner, so that the ratio of leaf area to leaf weight (specific leaf area) is higher. Hence, more light energy can be captured per unit leaf weight.
- 3) The distribution of plant weight between aerial and subterranean plant parts is generally different for plants grown in shade - they often display relatively more shoot to root than plants grown at high PFDs.
- 4) Internode extension is more in plants grown in shade than in plants of the same species grown at high PFDs.
- 5) In addition to these features, there are differences between the photosynthetic systems themselves; the most notable is that the light harvesting pigments differ in proportions of chlorophyll a to b.

A distinction should be made between acclimation to shade and adaptation to shade. Acclimation is essentially a short term phenomenon in which development of new growth is affected by growing conditions. Adaptation on the other hand is generally used to convey an evolutionary process whereby some plants show specific, genetically determined features which confer fitness in a particular circumstance. Björkman and Holmgren's study (1963) of sun and shade ecotypes clearly illustrates the difference between these phenomena.



More recent work has suggested that the effect of shade on plant development is not simply the effect of a reduced photon flux density or a shortage of assimilate. Instead it seems to be coupled to the perception by the plant of the R/FR in the incident radiation. Perhaps the most important and recent work on this subject is by Smith (1981, 1983) in which he showed that some of the features of adaptation to shade are produced even in bright light so long as the R/FR is similar to that found in the shade of leaf canopies. It is not at present clear whether all morphogenetic adaptations to shade are triggered by R/FR or merely by an overall reduced photon flux density.

For forest trees of TMF, several different evolutionary responses to the varying light regime may be recognised, but are here conveniently reduced to three major categories:

- 1) Light demanders, or obligate sun plant;
- 2) Shade tolerators, or facultative sun/shade plants;
- 3) Shade requirers, or obligate shade plants.

Shade requiring, flowering plants are rare, although many lower plants may be in this category. This thesis is restricted to light demanders and shade tolerators especially tropical trees in their early stage of growth. Most analyses of plant response to shade have been carried out on temperate herbaceous species and very little is yet known about tropical timber species.

### 3.1 Light demanders and shade tolerators

Natural forests produce their own microclimates and below the main canopy there are many shade tolerant and light demanding shrubs, herbs, tree seedlings and saplings. The young stages of most of the forest trees, even large emergents, are capable of mere existence in the dim layer : there they may "sit" for years making little or no growth, waiting for the chance of an opening in the canopy through age or wind (Langdale-Brown *et al.*, 1964). Within these forests, grasses



are of minor importance, and those that do occur are well adapted to shady existence.

The trees of TMFs have been crudely divided into two groups depending on the type of seeds they produce, the way these seeds germinate, and the means whereby these seedlings become established (Gómez-Pompa and Vázquez-Yánes 1974). The first and largest group includes those tree species that germinate and produce successful seedlings only in the discontinuous and unstable habitat created in gaps of fallen trees (Vázquez-Yánes and Orozco-Segovia 1982) and they are called light demanders (Whitmore 1975). The second group includes those that regenerate in the shade of the TMF canopy and are called shade tolerators.

Collectively, light demanders have been referred to in a variety of ways, including "biological nomads" (Van Steenis 1958), "Weed trees" (Corner 1954), or "pioneer species", appearing in open spaces before other species (Whitmore 1975, 1978, 1982). It is alleged that those species which require gaps for regeneration cannot grow up under their own shade, and both groups differ in several characteristics of seeds and seedlings (Whitmore 1975).

Although species belonging to both groups have long been known to tropical foresters and ecologists (Troup 1921), the physiological basis of the differences between light demanding and shade tolerating species of TMF remains largely uninvestigated (Whitmore 1975). What is known, is that the light demanders produce very large amounts of small seeds which remain dormant under intact canopies, and germinate to become seedlings only when a sizeable light gap is formed (Whitmore 1975, Vázquez-Yánes and Smith 1982). Their seedlings show a rapid height growth soon after germination in the gap; this rapid height growth is thought to be an advantage in competition for light : individuals falling behind become shaded and die, as these seedlings are incapable of living and growing under canopy shade-light (Vázquez-Yánes and Smith 1982). Their wood is of low density and pale in colour. Example of these is balsa wood (*Ochroma lagopus*) which has the lightest known wood (Whitmore 1975). Wherever gaps occur in the TMF canopy,



communities of fast growing, light demanding species may become established (Lawton 1976). Onyeagocha (1962) described Sapoba forest in Nigeria and classified light demanders to include *Triplochiton scleroxylon*, *Chlorophola excelsa* and *Terminalia ivorensis* of the emergents. Other well known light demanders in West Africa include *Macaranga hurifolia*, *Trema guinesis* and *Musanga cecropioides*. They tend to be short lived, and appear in the forest following a more or less extensive disturbance (Dosso et al., 1981). Human perturbation of forests has produced a huge increase in pioneer tree abundance (Vázquez-Yanes and Smith 1982).

On the other hand, shade tolerant species are characterized as a class by large seeds with substantial food reserves. Synnott (1975) estimated the fat content of *Entandrophragma utile* and found 30% fat in seeds. These seeds have no or only a brief period of dormancy and viability (Richards, 1952) and are able to germinate in deep shade of the forest floor. The seedlings often persist, growing slowly or not at all, in the dense undergrowth shade, marking time till a gap occurs above them. Jones (1956) did a 1% enumeration of Akure forest in Nigeria and described seedlings of shade tolerant species as those which can survive for several seasons in fairly dense shade. The list includes *Khaya ivorensis*, *Lovoa trichilioides*, *Gaurea*, *Cedrela* and many others. He stressed that some of the middle and lower storey species are truly shade tolerant. Timber of shade tolerant species is typically dense and dark e.g. *Khaya senegalensis* which is the heaviest of the African mahoganies (Irvine 1961). It is for their timber qualities that the shade tolerant species especially mahoganies have been prized in the timber trade, and this has led to their almost virtual extinction in some areas.

Autecological characteristics of species belonging to both of these groups have been studied for many temperate zone species (Bourdeau and Laverick 1958; Loach 1967, 1970; Wallace and Dunn 1980) and were recently summarized by Bazzaz (1979). Comparatively little is known about the autecology of tropical tree species (Bazzaz and Pickett 1980; Mooney et al., 1980; Whitmore 1982).



### 3.2 Growth response to shade

In general, two types of growth responses to shade have been widely recognised:

- (1) Light demanders: extreme extension growth of stems and petioles, reduced branching (enhanced apical dominance), reduced leaf area, reduced leaf thickness, increased specific leaf area (SLA) due principally to the decrease in leaf thickness (Grime, 1966);
- (2) Shade tolerators: little or no stimulation of extension growth (sometimes inhibition), increased leaf area, increased leaf thickness, increased SLA due to increased leaf area, increased chlorophyll content, and increased complexity of photosynthetic machinery (Grime 1966, Boardman 1977).

These modifications are physiological responses to shade which are initiated whenever an individual plant, or part of a plant becomes shaded, and may continue for days or weeks (Smith, 1983).

Limited work has been carried out on tropical plant species of agricultural importance such as coffee, cocoa, tea and bananas (e.g. Murray 1961; Murray and Nichols 1966). Murray and Nichols (1966) investigated cocoa yield in relation to shade, they stressed that "if mineral nutrition is poor, shade is necessary; as nutrition improves so does light requirement for yield increase".

Growth in response to shade has been investigated to a limited extent. For instance Nicholson (1960) investigated five dipterocarp species in Malaya: he showed that these species required shade for establishment, and later, they showed decreasing tolerance and responded to full light after about 18 months by rapid growth. Edmiston (1970) showed that *Ormosia krugii* was capable of carbon fixation at low PFD but developed faster at higher PFDs. Ampofo and Lawson (1972) showed that *Afrormosia elata* responded by overall growth in partial shade.



Wadsworth and Lawton (1968) remarked on the scarcity of information on growth rates of forest tree seedlings in shade. Okali (1971, 1972) responded by analysing rates of dry matter production of four West African forest tree seedlings : *Chlorophola excelsa*, *Musanga cecropioides*, *Terminalia ivorensis* and *Ceiba pentandra* compared to *Helianthus annuus*. He found that only *Ceiba pentandra* had unusually high net assimilation rates in the experiment, which did not differ significantly from the value found for *Helianthus*. In relation to shade, he concluded that it was the woody habitat, not the differential adaptation to light that was mainly responsible for the lower growth rates of the woody plants when compared with *Helianthus*. Also, the high light requirement of the tree seedlings was consistent with their role as pioneers in regeneration of the natural West African TMFs. Fasehun and Audu (1980) compared growth in nursery grown seedlings of *Gmelina arborea*, *Terminalia superba*, *Terminalia ivorensis* and *Chlorophola regia*. They showed that net assimilation rate (NAR) for *Terminalia ivorensis* was similar in magnitude to those reported by Okali (1971) for this species; also that NARs for four tropical hardwood species lie below or within the range of maximum values for woody species as was shown by Jarvis and Jarvis (1964).

Synnott (1975) investigated the factors affecting the regeneration and growth of seedlings of *Entandrophragma utile* in Budongo forest. He showed that the seedlings were healthier when grown under at least some shade, and also that these seedlings grew more slowly under the forest canopy conditions compared to the nursery conditions.

Fetcher et al., (1983) conducted an experiment with *Heliocarpus appendiculatus*, a pioneer or large gap species of TMF in Costa Rica, and *Dipteryx panamasis*, a small gap species. Seedlings were grown in full sun, partial (80%) shade, and full (98%) shade. After one month of growth, they were switched between environments for two months. The result was that height growth of the light demander was affected by irradiance: being increased in response to full shade and decreased in full sun. The light demander also exhibited greater changes in leaf thickness, specific leaf weight, and stomatal density than did the shade



tolerator. Survival of *Heliocarpus* seedlings was only 49% in full shade, whereas *Dipteryx* had 100% survival.

### 3.2.1 Morphogenesis

It has been known for some time (Blackman and Wilson 1951; Evans and Hughes 1961; Huxley 1967) that many plant species display surprisingly consistent relative growth rate (RGR) over a wide range of PFDs when they are grown from seed, and that this is achieved through adaptations in morphology (Corré, 1983b). Van Dobben *et al* (1981) confirmed this reaction in *Phaseolus vulgaris*.

The major adaptation to shade is the formation of thinner leaves with a high water content, resulting in a higher SLA. Another important adaptation is the decrease of the root weight ratio in shade. Mostly, the dry matter not used in the root growth will be distributed as stems and petioles, and not leaf blades, so this does not contribute indirectly by saving carbohydrates since root respiration in general exceeds stem respiration (Corré 1983a). On a unit weight basis the leaf weight ratio can remain constant over a wide range of PFDs.

Increasing SLA combined with a generally equal leaf weight ratio (LWR) leads to an increase in leaf area ratio (LAR) and this relative increase in leaf area can compensate, at least partially, for a lower photosynthetic rate per unit of area. It seems possible that shade species do better in this respect than sun species. Blackman and Wilson (1951) suggested that the shade plants should be defined as "a species which a reduction in light intensity causes a rapid rise in leaf area ratio from an initial low value in full sunlight", but this definition has never been confirmed (Corré 1983a) and is even contradicted by Grime (1965) who supposes that many sun plants even show a more pronounced adaptation to low PFD than shade plants do. This is supported by the experiment of Loach (1970) who found a great adaptation of the LAR in *Liriodendron tulipifera* than in three shade tolerant tree species. Loach also cited examples of several shade tolerant tree species which showed such less adaptation in terms of leaf thickness than non-tolerant species did. On the other hand there



are examples of sun species that do not show a good adaptation to a low PFD such as *Helianthus annuus* (Hiroi and Monsi 1963). Loach (1970) found a small increase in LWR in shade tolerant *Fagus grandifolia*.

### 3.2.2 Photosynthesis and respiration responses in relation to shade

Various authors have compared photosynthesis in sun and shade species or ecotypes. For instance, photosynthesis per unit leaf area at high PFDs was appreciably lower in shade adapted ecotypes of *Solidago virgaurea* (Björkman and Holmgren 1963), *Rumex acetosa* (Björkman and Holmgren 1966) and *Solanum dulcamara* (Gauhl 1976) which had been grown at high PFD, than it was in the sun adapted ecotypes grown at the same PFD. On the other hand, the initial slope of the light response curve of plants grown at low PFD was somewhat steeper in the shade adapted ecotypes, at least in *Solidago virgaurea* (Björkman and Holmgren 1963), but there was no significant difference in light compensation points, nor in dark respiration. Besides, a comparison of other herbaceous species, like *Plantago lanceolata* and *Lamium galeobdolon* (Björkman and Holmgren 1966); *Calendula officinalis* and *Impatiens parviflora* (Greon 1973); and *Cirsium palustre* and *Geum urbanum* (Pons 1977), did not show these differences. Greon and Pons concluded that it is not possible to explain the absence of sun plants in shaded habitats in terms of efficiency of utilization of light energy.

In *Phaseolus vulgaris*, Crookston et al., (1975) undertook to determine more clearly the nature of photosynthetic reduction in leaves grown at low PFD. The cultivars were grown at PFDs near photosynthetic saturation for beans ( $390 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and also at fluxes commonly found in the lower regions of field canopies ( $55 \mu\text{mol m}^{-2} \text{s}^{-1}$  in the 400-700 nm waveband of PAR). They found that the magnitude of photosynthetic reduction due to shading averaged 38%.

Another possible difference between sun and shade plants lies in the rate of respiration at very low PFDs. Mohmoud and Grime (1974) found that *Deschampsia flexuosa*, *Festuca ovina* and *Agrostis tenuis* (in order of decreasing shade tolerance) have only negligible differences in light compensation points and in net photosynthesis, based on whole



plant dry weights, at low PFD. However, at PFDs less than the compensation point, the respiration losses, calculated from weight losses of whole plant during a period of four weeks, differed widely: the most shade tolerant species showing the smallest losses. The same phenomenon was reported by Willmot and Moore (1973) in *Silene alba* and *S. dioica* grown at high and low PFD, where the shade tolerant *S. dioica* showed the smallest dark respiration rate.

In tree seedlings, Loach (1967) found much higher respiration losses in *Populus tremula* grown at low PFD than in some shade tolerant trees and Hutchinson (1967) showed that seedlings of shade tolerant plant species could survive in absolute darkness much longer than sun species could, which also points to differences in respiration. Moreover, a low respiration rate may lead to the maintenance of a higher soluble carbohydrate content, which gives the plant a higher resistance to fungal attack, a very important cause of death in shaded habitats (Hutchinson 1967, Vaartaja 1962).

There is limited work on tropical tree seedlings in this respect such as Fasehun and Audu (1980), Osonubi and Davies (1980), Robichaux and Percy (1980), Bazzaz and Carlson (1982), Percy and Calkin (1983) and Ladipo *et al.*, (1984); this will be discussed in detail in later chapters. It should be pointed out that the variability in the energy environment in TMF is related mainly to the amount of energy received at the top of the canopy, its attenuation by the vegetation and the way in which it is dispersed. The degree of flexibility of different species to acclimate to the light conditions at the forest floor must itself be related to the level of environmental variation of the habitat in which the species are normally found.

### 3.3 Response to R/FR ratio

As discussed in the previous chapter (Chapter 2), the shade under canopy leaves is characterized by a reduction in the red/far-red ratio (R/FR). Plants appear to detect shade by reference to the state of phytochrome, a molecule which changes its state according to R/FR. Many responses to shade are known to be initiated by R/FR. The



discovery of the red-far red reaction was first made by Borthwick *et al* (1952) working on germination of lettuce seeds. Since then numerous other processes have been found to be controlled by light quality in a similar way.

Morgan and Smith (1981) discussed several methods of simulation of naturally occurring changes in R/FR ratio for studies in controlled environments of the effects of twilight and vegetational shade. They pointed out that the simplest and most unsatisfactory method is to compare the effects of white fluorescent light alone (R/FR 3-6) with those of either incandescent light, or incandescent light alone (R/FR 0.7-0.8). They stressed that fluorescent light does not simulate daylight well, whilst light from tungsten filament lamps is only equivalent to very sparse shade. This is because in terrestrial environments the highest R/FR ratio is found in daylight (R/FR  $\approx$  1.2); R/FR ratios in shade and twilight are lower (Section 2.5.2). Vázquez-Yanes and Smith (1982) referred to R/FR values measured in the rainforest of Los Tuxtlas, Mexico using a field spectroradiometer, of 0.3 to less than 0.02 in dense forest parts. Consequently Morgan and Smith (1981) advised that the problems associated with simulation of R/FR ratio in controlled environment can be partially overcome if fluorescent light is used as a background white light source for a constant spectrum and fluence rates of PAR, and far-red light (>700 nm) is added from either incandescent light as was achieved by Heathcote *et al*; (1979) or using far-red emitting fluorescent tubes (Dietzer *et al.*, 1979). However, full simulation of spectral photon distribution of natural radiation poses major technical problems, and has yet to be achieved (Morgan and Smith, 1981).

### 3.3.1 Seed germination

The influence of shade on the germination of seeds in tropical ecosystems requires study, but is outside the scope of this present work. However, a brief review on this subject would serve a useful purpose in the understanding of the seedling response to R/FR in later chapters.



It is now well established that seed germination in some species is affected by the presence or absence of light as discussed by Mayer and Poljakof-Mayber (1963). For instance, Black (1969) reported on work over a century ago where records of over 600 species of seed were stated to be light sensitive, and it was the subsequent use of light sensitive lettuce seeds that led to the discovery of the phytochrome system (Borthwick *et al* 1952). Following these basic discoveries, research was intensified and it has become apparent that the operation of phytochrome in seeds is very complex. In some species there exists light sensitized germination known as positive photoblastic (germination promoted by white light), and other species have dormancy mechanisms based on light quality especially the R/FR ratio acting through the phytochrome system.

The increased far-red/red ratio under forest and other vegetation canopies relative to that in the open inhibits germination in some species (Taylorson and Borthwick, 1969). This possibly suggests that in nature, phytochrome may act to detect exposure to light thereby inhibiting germination in seeds shaded by vegetation, allowing germination when the vegetation is cleared or burned. However, seeds of many species show large variability in their germination behaviour.

Of special interest to this study is work on TMF species. Vázquez-Yanes (1980) observed that germination of two shade-intolerant species was inhibited by the shade-light of rainforest canopy whilst germination was fully promoted when the shade-light was filtered through a red narrow band-pass filter. In another experiment, Vázquez-Yanes and Smith (1982) studied germination under simulated natural light spectra in four growth chambers in which PAR was kept constant at  $40 \mu\text{mol m}^{-2} \text{s}^{-1}$ , whilst R/FR ratio was varied from 0.2, 0.23, 0.58 and 2.3 using a gamma spectroradiometer. They found that germination of *Cecropia obtusifolia* and *Piper auritum* was also under photocontrol. *C. obtusifolia* germinated more slowly under low R/FR, but with sufficient time most seeds germinated in all chambers. For *P. auritum* the effect of low R/FR was more drastic and some of the seed samples remained dormant under simulated dense canopies.



The conclusion from this experiment was that germination was triggered when R/FR ratio of the incident light increased due to a reduction of the green canopy density and exposure to simulated light canopies retarded and reduced germination in both species. Also, experiments with alternate red and far-red light treatments indicated need for longer periods of exposure to red light for germination. Subsequently, these reactions were related to the ecology of seeds in natural habitat. The seeds of both *C. obtusifolia* and *P. auritum* can remain dormant in darkness or soil for more than a year possibly waiting for a light gap to form in the canopy. However, the probability of a light gap forming in any one place was about 1% per 100 years in the places Whitmore (1978) studied.

Vázquez-Yanes and Smith (1982) also stressed that changes in light quality seem to be the only controlling mechanism acting in natural conditions in relation to light gap formation, and indeed the most efficient one because it permits germination to be timed precisely with gap formation when plants of many species may compete for establishment in a new open space. The fact that long periods of continuous intermittent red light treatment were needed for both species to initiate germination may possibly be related to the ability of the seeds to determine the size of the gap, and to differentiate it from a normal sunfleck reaching the soil on the forest floor. Thus a small light gap, or a sun fleck will give a short period of unfiltered light exposure to the soil (and therefore a high R/FR) but soon the filtered light (low R/FR) will re-impose dormancy. On the other hand, a large gap will permit a long period of unfiltered light exposure (high R/FR) on consecutive days with a much shorter period of filtered (low R/FR) light. However, Morgan and Smith (1981) pointed out that such light sensitive germination does not necessarily explain their natural distribution although it is highly suggestive. In another experiment Vázquez-Yanes and Orozco-Segovia (1982) showed that the tropical forest pioneer tree *Heliocarpus donnell-smithii* establishes only in the light gaps of the forest canopy. They showed that germination increased if temperature rises were above 31 °C, although the mechanism triggering germination is related to light quality.



### 3.3.2 Photomorphogenesis

#### 3.3.2.1 Stem extension

There is virtually no published work on the effects of R/FR ratio on growth of tropical tree seedlings. This review is based on observations on crop and herbaceous temperate plant species.

Downs *et al.*, (1957) were the first to demonstrate R/FR reversible control of stem development in light grown plants. A five minutes exposure to far-red light, at the end of an eight hour white (fluorescent) light photoperiod, increased internode extension up to 400% in a range of bean (*Phaseolus vulgaris*) varieties, sunflower (*Helianthus annuus*) and morning glory (*Ipomea hederacea*). When far-red light was immediately followed by five minutes red light, the effect was fully reversed. Similar observations have been reported many times in more species. In wild plants the extension response has clear ecological correlations: aggressive ruderal herbs appear to have a strong response whilst woodland herbs have almost no response at all (Smith 1981).

This subject has recently been reviewed by Morgan and Smith (1981) who pointed out that it was unfortunate that most of the species studied were crop plants, and lamp combinations used produced a range of R/FR most of which is not found in terrestrial nature. They also stressed that there was evidence to suggest that the response to R/FR of simulated shade might change with plant age.

#### 3.3.2.2 Apical dominance

Closely related to stem extension growth is apical dominance. Many field observations have shown that plants growing in open habitats branch profusely; whilst shaded plants may show complete apical dominance (Bogorad and McIlrath 1960; Kasperbauer 1971; Tucker and Mansfield 1972, and resume' by Longman and Jeník 1974). In controlled environments, R/FR ratio has been found to exert a remarkable degree of control over this response, but there have been no reports in



realistic shade simulation. Fitter and Hay (1981) remarked that sustained extension growth might be important for canopy tree seedlings.

### 3.3.2.3 Leaf morphology

The effects of R/FR ratio on leaf thickness or specific leaf area (SLA) is not yet clear (Corré 1983b). Thinner leaves under a low R/FR ratio were reported by Holmes and Smith (1977c), McLaren and Smith (1978) and Kasperbauer (1971), but no effects were found by Morgan and Smith (1981b). Fitter and Ashmore (1974) found a lower SLA in artificial shade in *Veronica persica* than in *Veronica montana*, but a much higher specific leaf area in an experiment with natural shade.

### 3.3.3 Photosynthesis and respiration

Much less is known about possible involvement of phytochrome in the development of the structural and biophysical characteristics of photosynthesis or respiration. Most experiments have used artificial shade, and very little is known about any influence R/FR ratio might have (Corré 1983b). However, Björkman (1973) suggested that quanta above 700 nm may be important in the photosynthesis of extreme shade plants, and McCree (1981) estimated that the region above 700 nm might account for as much as 7% of the total quantum flux density available for photosynthesis by shade leaves inside of a tree canopy. Since virtually nothing is known about the photosynthetic action spectra of TMF plants, it is still impossible to determine how important the quanta of radiation beyond 700 nm might be for photosynthesis. Besides this is outside the range of absorption by chlorophyll.

Kasperbauer and Peaslee (1973) found that in tobacco, a short red or far-red illumination at the end of the light period did not have any influence on the subsequent photosynthetic rate on the basis of leaf area, although there was a marked difference in morphology, for example leaf thickness. To date, no evidence is available on the possible effects of long-term illuminations with light of a low R/FR ratio.



In a range of herbaceous sun and shade plants *Plantago major*, *Galinsoga parviflora*, *Urtica urens*, *Polygonum lapathifolium*, *Urtica dioica*, *Circaea lutetiana*, *Geum urbanum*, *Impatiens parviflora*, *Scrophularia nodosa* and *Stachys sylvatica* grown under two R/FR ratios; Corré (1983) found that full photosynthetic capacity was reached at about  $140 \mu\text{mol m}^{-2} \text{s}^{-1}$  in all the species and tended to be higher in sun species. It was also lower in plants grown under a low R/FR ratio, except for *Urtica urens*, in which it was slightly higher. The photosynthetic efficiency varied appreciably with species; he reported that the efficiency was not influenced by the ratio except *Plantago major*, where it was lower in plants grown under a low R/FR ratio. He then suggested that this was probably because the leaves grew more upright under low R/FR ratio.

On the other hand, there is evidence that respiration can be influenced by the R/FR ratio. Leopold and Guernsey (1954) found that under red light, dark respiration decreased in the oat mesocotyl and the pea stem, and that there was a concomitant decrease in cell extension, whereas under far-red light, dark respiration and cell extension increased. Moreover, in red light dark respiration in leaves of barley (a long-day plant) increased, but in leaves of *Xanthium commune* and Soybean (both short-day plants) it decreased: far-red light had the opposite effect. Hock and Mohr (1964) found that dark respiration in leaves of *Sinapis alba* was stimulated under both red and far-red light. The increase was larger under far-red light after a short illumination, and even larger when illumination exceeded approximately ten hours.

Although not indisputable, it seems reasonable to suppose that the R/FR ratio has no direct effects on respiration rates, but only indirect effects through its influence on energy-demanding processes, such as stem elongation (Corré 1983).



### 3.4 Others

Apart from phytochrome, there is one other known photoreceptor which is concerned with photomorphogenesis. It is a blue light receptor sometimes called cryptochrome. This receptor shows no photoreversibility as it exists in only one form. Smith (1981) argues that it could not therefore have a role in detecting vegetational shade. Besides, the blue light receptor absorbs in ultraviolet and blue wavelengths that do not have a photoreversible effect, and furthermore the ultraviolet effect is small, because of attenuation by atmospheric ozone (Morgan and Smith 1981a). The blue light receptor could only be useful in detecting the light quantity not the quality of light because in nature, changes in light quality never occur without simultaneous changes in light quantity (Smith 1983). The naturally occurring spectra can only be resolved with a combination of two photoreceptors - one for light quality and the other for light quantity (Morgan and Smith 1981).

It does however appear that the blue light receptor has a role in seedling development, especially in the hypocotyl elongation (Morgan and Smith, 1981). Chlorophyll is presumed to have only indirect effects on morphogenesis via energy transduction (Morgan and Smith, 1981a).

Morgan and Smith (1981) have summarized some of the other photomorphogenic changes shown by plants in response to an increase in the proportion of far-red light in incident radiation as shown in Table 3 below:

It is clear that an influence of R/FR can be demonstrated on a wide range of plant responses.



TABLE 3

Developmental Factor	Effect	Species	Light treatment	References
Petiole length	+	Strawberry	End-of-day far-red	Vince-Prue (1976)
	+	<i>Cucurbita pepo</i>	Simulated shadelight	Holmes and Smith (1977c)
Leaf length	+	Tobacco	End-of-day far-red	Kasperbauer and Hiatt (1966)
	-	Mosses	Simulated shadelight	Hoddinott and Bain (1979)
Leaf area	-	<i>Chenopodium album</i>	Tungsten/fluorescent	Holmes and Smith (1975)
	-	<i>Rumex obtusifolius</i>	Simulated shadelight	McLaren and Smith (1978)
Stem dry weight	+	Tomato	Tungsten/fluorescent	Hurd (1974)
	+	<i>Cucurbita pepo</i> (hypocotyl)	Simulated shadelight	Holmes and Smith (1977c)
Transition to climbing form	-	<i>Phaseolus</i>	Nightbreak far-red	Kretschmer <i>et al.</i> (1977)
Flowering	+	Wheat	Tungsten/fluorescent	Friend <i>et al.</i> (1961)
	+	Strawberry	Tungsten/fluorescent	Collins (1966)
Senescence	+	<i>Marchantia</i>	End-of-day far-red	DeGreef and Fredericq (1972)
Chlorophyll content	-	<i>Marchantia</i>	End-of-day far-red	Fredericq and De Greef (1966)
	-	<i>Rumex obtusifolius</i>	Simulated shadelight	McLaren and Smith (1978)
	+	<i>Veronica persica</i>	Simulated shadelight	Fitter and Ashmore (1974)
Free sugars/organic acids	+	Tobacco	End-of-day far-red	Kasperbauer <i>et al.</i> (1970)
Ethylene production	+	Peach	Natural shade	Erez (1977)

Some photomorphogenic changes shown by plants in response to an increase of the proportion of far-red light in the incident radiation (+ = stimulation, - = inhibition). From Morgan and Smith (1981).



## CHAPTER FOUR

### CHOICE OF THE SPECIES

As mentioned in the previous chapter, the widest possible range of shade tolerating and light demanding species were considered. The light demanders included *Maesopsis eminii* that is currently being used for enrichment planting in Mabira forest of Uganda, *Chlorophora excelsa*, *Nuclea diderrichii*, *Triplochiton scleroxylon*, *Terminalia superba* and *Terminalia ivorensis*. The shade tolerant species included *Entandrophragma angolense*, *Khaya ivorensis* and *Khaya senegalensis*. The light demanding sedge *Cyperus papyrus* was selected to contrast with the tree species. However, the choice depended on the availability of viable seed as reported in Chapter 7.

Eventually the list of tree species was reduced to only two: *Terminalia ivorensis* and *Khaya senegalensis*, both important timber tree species and currently being considered for further plantation forestry in West Africa.

In this chapter, a brief description of the ecological characteristics of the species is presented.

#### 4.1 *Terminalia ivorensis* A. Chev (Combretaceae)

*Terminalia ivorensis* is a well known West African tree as described by Lamb and Ntima (1971). Much work has also been advanced on the species characteristics (Longman and Jenik 1974) and its performance in plantation monoculture in Nigeria under the auspices of the West African Hardwood Improvement Project (Howland and Bowen, 1977).

This species is known to occur at various localities throughout the tropical moist forest and seasonal forest zones in West Africa from Guinea through Sierra-Leone, Liberia, Ivory Coast, Ghana, Nigeria to the Cameroons in Central Africa (Kennedy, 1936).



Habitat conditions as detailed by Lamb and Ntima (1971) can be summarized as follows:

(1) Rainfall: For optimum development, *T. ivorensis* requires high, well distributed rainfall above 1270 mm per annum. It is not drought resistant when young and is easily killed by drought within a few weeks of planting. However, its deciduous nature protects it in seasonal climates.

(2) Temperature: Mean annual temperature in the tropical lowland fluctuates between 20 °C and 33 °C; within this range, *T. ivorensis* can be successfully grown.

(3) Humidity: Relative humidity seldom falls below 50% during the dry season in its natural habitat. At air temperature of 30 °C this implies a saturation vapour pressure deficit (SVPD) of 2.1 kPa (=21 mbar).

(4) Altitude : *T. ivorensis* is a species mainly of low altitude, although it may be found growing at higher altitudes. In Ghana it grows up to 610 m while in Cameroon it can be found as high as 1219 m above sea level. In Uganda it has been included in a species trial in Kibale at an altitude of 1524 m, but it has not grown well. Elsewhere in Uganda at altitudes between 700 - 1200 m, it shows considerable promise on moist fertile soils. In general, it is a species likely to do best below 1200 m above sea level.

(5) Edaphic factors: Upland lateric loams in Sierra-leone, well drained loams in Ghana, sandy loams in Western Nigeria, clay loams in Tanzania (Willan 1966) and volcanic soils of British Solomon Islands (Leggate 1966) are most suitable soils for *T. ivorensis*. It is very sensitive to water logging, and does not do well in valley bottoms subject to long periods of inundation.

(6) Shade: *T. ivorensis* is a light demander and does not tolerate shade after germination (Lamb and Ntima, 1971). It is often found in the tropical moist forest conditions, but it is predominantly a tree of the seasonal forest zones; and is found mixed with *T. superba* where it



shows some of the latter's characteristics, being a strong (aggressive) light demander and a good colonizer of abandoned farms. It is an emergent of the upper storey of the seasonal forest. Because of its nature as a light demander, its distribution may reflect on the density of shade in the high forest. Bernard-Reverset (1978), classified *T. ivorensis* as a dense forest species. However in Nigerian seasonal forests of Ala and Akure-Afuso, densities of 0.14 stems/ha and in less deciduous forest of Idanie and Oluwa, densities of 0.0032 stems/ha were recorded (Mac Gregor 1934): an indication of the contribution of *T. ivorensis* to the canopy, besides the influence by man. In Ivory Coast, it is said to be abundant in the secondary and primary forests in deciduous forest zone especially in the transition to the moist forests. It also occurs in those parts deforested by shifting cultivation. In Ghana, it occurs with *T. superba*, *Celtis* spp. and *Triplochiton scleroxylon* whilst in Sierra-Leone it is characteristic of secondary forest. Natural regeneration is fairly good and most frequently met with where there is ample light such as a gap in the forest canopy or in areas cleared for farms.

#### 4.2 *Khaya senegalensis* (Desr) A. Juss

This species belongs to the family *Meliaceae* and is often referred to as the African Mahogany by timber merchants. Irvine (1961) reported that it is the heaviest of African mahoganies and was first known and exported from Gambia over a century ago. The name mahogany (Maogani) was applied to this tree in 1763 by Adamson in reference to a tree in Senegal. Later, a French botanist Desrousseaux 1789 gave it the name *Swietenia senegalensis* because of its close resemblance to *Swietenia mahogani*. When Adrien de Jussieur in 1830 described the genus *Khaya*, he transferred *Swietenia mahogani* (Desr), giving the name *Khaya senegalensis*. African mahogany (*Khaya* spp) reached Liverpool as early as 1835 (Lamb 1966).

*Khaya senegalensis* has a wide geographical distribution : from Senegal in the West through Gambia, Upper Volta, Guinea Bissau, Guinea, Sierra-Leone, Ivory Coast, Dahomey, Niger, Northern and Southern Nigeria, through North-Central Africa to Sudan and Uganda in East Africa.



It is a common and well known dry-zone mahogany. It occurs in tropical moist forests as well as savanna. Its best habitat is the banks of streams (riverline species). Its soils and water requirements are comparatively modest and any little valley or moist hollow is sufficient.

Kennedy (1936) referred to this species as probably the largest tree of the savanna regions. It is known to be gregarious and to form wide spreading crowns in the open (Kennedy 1936, Irvine 1961). Like most other savanna species, it is deciduous (Eggeling 1940).

Natural regeneration is poor and root suckers were the main methods of reproduction (Kennedy 1936).

Richards (1952) describing the genus *Khaya* pointed out that *Khaya* species are found both in closed forest and savanna: *Khaya ivorensis* and *Khaya anthotheca* in evergreen forest, *Khaya grandifoliola* in the dry forest and *Khaya senegalensis* in the savannas. He stressed that "these 'vicarious' species should be regarded as ecotypes".

In relation to shade, the closely related *Khaya ivorensis* is a well known shade tolerator. Information on *Khaya senegalensis* is less definite on this point, but since the species is a constituent of the woodland savanna climax, it can be presumed that its seedlings are also shade tolerant. Its possession of dense wood and large seeds is a further indication that this species is a shade tolerator, and in this respect it contrasts with *Terminalia ivorensis*.

#### 4.3 *Cyperus papyrus* L., Family Cyperaceae

*Cyperus papyrus* is a large aquatic sedge with stems (culms) up to 5 metres high (Gaudet 1977). Recent research indicates that papyrus is among the most productive plants in the world. In general, the swamps at higher altitudes, near the upper limit of papyrus of about 2000 m have the highest biomass; these higher altitude swamps such as those of Lakes Naivasha and Bunyonyi may be able to maintain large amounts of standing vegetation because the lower temperatures at high altitudes reduce the loss of carbon through respiration. As temperature falls, the rate of respiration declines more rapidly than



the rate of photosynthesis so that the plant ends up with a carbon balance which is more positive. *C. papyrus* will regrow rapidly after it has been harvested and can probably regain its original biomass within 9 months to a year in most cases (Jones 1983a). This would mean that the annual production of the most productive swamps is about 30 t/ha, a value that compares very favourably with forests as a source of biomass.

Other special features of papyrus are:

- (1) Like many tropical grasses, it displays  $C_4$  photosynthesis (see Downton 1975, Jones and Milburn, 1978).
- (2) The roots of papyrus harbour nitrogen fixing organisms which provide nitrogen in a form that the plant can take up as nutrient.
- (3) Its roots are found in anoxic environments; but, the plant has overcome this by developing a system of large inter-connecting spaces between the cells, through which oxygen can diffuse.
- (4) The culms are green and photosynthetic.

*Cyperus papyrus* has a very restricted distribution and is native only to the African continent, Madagascar and Israel (Weber 1942, Thompson 1976a). Most papyrus swamps are now concentrated in Eastern and Central Africa.

The most extensive papyrus swamps are associated with large shallow lake systems, and the Upemba swamps in Southern Zaire are one of the examples of this type (Thompson 1976b). The rest are in the Upper Nile swamps and are better known as the Sudd or floating mats where papyrus forms a virtual monoculture of over one million hectares (Rzóńska 1974, Thompson *et al.*, 1979); Lake Naivasha in Kenya (Gaudet 1975, 1977); the Victoria basin (Lind and Visser 1962, Gaudet 1977); Lake Kyoga and the lakes of South West Uganda including Lake Bunyonyi (Denny 1973), Lake George, and all the major river banks in Uganda such as Katonga, Kafu and Kagera and of course the Nile.



In other parts of Africa, it is found in Rwanda and Burundi (Jones 1983a), Lake Chad, in the North and as far South as the Okovango swamps in Botswana. Little information is available for West and Southern Africa.

The papyrus plant is of historical interest : it was an important multi-use material (food, boats, mats, etc.) in ancient Egypt. It is best known as one of the earliest (3000 B.C.) writing surfaces of ancient Egyptians, Greeks and Romans (Weber 1942, Hepper 1978, McGovern 1981 and Jones 1983a). Papyrus is the origin of the modern word paper, which is derived from the Greek name for the plant papyros, and the Greeks called the pith from which paper is made, biblos a term later applied to all books and, subsequently the Bible (Hepper 1978). Ancient paper from papyrus was made by overlapping and cross-laminating strips of the pith and pressing to dryness to form a mat with a lattice structure (McGovern, 1981). However, its use was abandoned in favour of parchment and vellum both made from animal skins because of its liability to decay (Hepper 1978, Jones 1983a). At the time papyrus grew abundantly along the Nile and was cultivated along its banks by the Egyptians until the pressure to use the fertile swamp soils for other crops was so intense that it was cleared and eventually almost completely disappeared from Egypt (Jones 1983a).

However, as wood pulp becomes increasingly expensive and hard to obtain, manufacturers are now turning to other materials. It is a historical oddity, therefore, that pulped papyrus is now being considered a suitable alternative, nearly 2000 years after its use was abandoned (Hepper 1978). Also, technology originally designed to convert peat into an efficient solid fuel in Ireland may soon be turning vast African swamps of papyrus into vital fuel for hard pressed Third World countries that are fortunate enough to have this resource. According to Jones (1983a) "our increased knowledge of papyrus has come at a time when we have become acutely aware of the 'other energy crisis' particularly in Central Asia and Africa". This crisis is due to the rapid disappearance of Tropical forests (Chapter 1, section 1.2) as a major source of fuel, either burned as wood or converted to charcoal, the main source of energy in much of urban Africa (Jones 1983a). So



papyrus, which in many cases grows on peat, is an obvious alternative, in form of briquettes with a density slightly greater than that of wood.

The presence of vast amounts of papyrus in some parts of Uganda and Madagascar where the present rate of forest conversion to other uses has been estimated at twice the world average total (Jackson 1983) is a blessing in disguise. These countries should consider seriously, reducing pressure on the remaining TMFs by embarking on alternative resources such as the proposed papyrus briquettes (Jones 1983a) through scientific management of papyrus swamps.



## CHAPTER 5

### **THE EFFECT OF SHADE ON GROWTH: A PRELIMINARY GLASSHOUSE EXPERIMENT.**

In Chapter three, it was reported that the response to shade is generally different for plants found in open habitats compared to those found in shaded habitats. So far, it has been pointed out that the differences between light demanding and shade tolerating tropical tree species remains largely uninvestigated. It was also pointed out in Chapter Four that *Terminalia ivorensis* and *Khaya senegalensis* belong to the two contrasting groups above.

In this chapter, a preliminary investigation is reported. It was carried out on the above species to assess their response to simulated shade in the glasshouse. It was necessary to investigate these species to assess whether they behaved differently under similar conditions, and also to assess whether there actually exist differences in response to shade. Different water regimes were also included in the experiment to examine the possibility that these species might differ also in relation to flooding tolerance (flooding is frequently a problem in establishing tree seedlings in wetter places e.g. lake shore regions of Lake Victoria in Uganda). However, flooding proved to be of only minor importance in these short term experiments.

Thereafter, the observed responses to shade were further investigated in a more closely controlled environment as will be presented in later chapters.

#### **5.1 Materials and Methods**

##### **5.1.1 Design of shade screens and the light regime under them**

It is now well recognised that forest shade is characterized by reduced photon flux density of photosynthetically active radiation (PAR) and low R/FR ratio. In this experiment, no attempt was made to separate these two factors, but care was taken to ensure that an



appropriate reduction in R/FR ratio did accompany the reduction in PAR.

To simulate forest shade, a range of green celluloid filters (Northern Light, Edinburgh) : Cinemoid 21, 22, 23, 24, 38, 77, and BBC green was chosen and tested across the broad waveband 400-750 nm using a standard laboratory spectrophotometer (Pye Unicam SP800, Cambridge) and at specific wavelengths 660 nm and 730 nm using a Quantum Spectroradiometer (QSM-2500, Techum Instruments, Sweden). In the latter case, the filter was simply interposed between an incandescent bulb (60 W) and the sensing head.

From these trials was selected Cinemoid No. 22 'Moss green' as a filter with which to construct shade screens. Its overall transmittance in the photosynthetically active part of the spectrum was about 20 % whilst its R/FR transmittance was suitably low.

To obtain a range of shade, screens were constructed using 1, 2 or 3 layers of filter material, the latter being augmented by 4 layers of muslin. Both muslin and white-washed glasshouse glass were found to be near-neutral filters.

Six wooden frames (0.63 x 0.63 x 0.63 m) were constructed and the filter material mounted on them. A ventilation gap (0.19 m) was left at the bottom.

#### 5.1.2 Plant material

*Khaya senegalensis* was raised from seed obtained from Nigeria, collected at Tabeta-Mokwa (index No. 5966). These seeds were germinated on the mist bench in the glasshouse. *Terminalia ivorensis* was supplied as seedlings from the Institute of Terrestrial Ecology (ITE), the seed being of Nigerian provenance (index No. 6688, Okum).

#### 5.1.3 Cultivation regime

1) Soil: On 25/6/82 the plants were transplanted into plastic containers (Long Tom No. 4) in a UC 50:50 sphagnum peat compost and sand, with



a pH of about 5.5. After 10 weeks of growth, all the seedlings were divided into five groups (based on height) of 15 plants of each species.

2) Water: To explore possible interactions between shade and water supply, three water regimes were employed. On 5/8/82, the seedlings were subjected to three different water regimes under each of the filter layers: 1, 2 and 3, where 15 plants of each species were raised. Of the 15 plants, five were subjected to flooding conditions, five were watered once a week (dry condition) and the other five were watered once a day. The flooded condition was maintained by enclosing the soil in polythene bags contained within the plastic containers.

3) Light, Temperature and Relative humidity: Temperature and relative humidity were partially controlled in the glasshouse. Day temperatures were usually about  $25^{\circ}\text{C}$  whilst night temperatures were about  $20^{\circ}\text{C}$ . Relative humidity was usually over 50 %. On the other hand, light was difficult to control, bearing in mind that this is one of the most fluctuating environmental variables (Anderson 1966), depending on the naturally-fluctuating weather conditions outside the glasshouse. At this time of the year, photoperiod was about 14 hours.

A quantum sensor was tracked along inside the shade screens to examine the distribution of photon-flux under them. These trials established that there was a considerable fall off at the edges amounting to about 20 % of the photon flux in the centre. They also enabled the light levels to be defined in relation to that on the glasshouse bench, which in the later section will be referred as the 'open'. Levels of about 32 %, 18 % and 5 % of the open condition were recorded under 1 layer, 2 layers and 3 layers respectively on most sunny days (see Fig. 5.1).

Measurements of absolute light levels were made near noon once a week. The lowest recorded values were, under 3 layers of filter material with four layers of muslin,  $26 \mu\text{mol m}^{-2} \text{s}^{-1}$  on 27/8/82; whilst the highest value recorded in the glasshouse was  $1120 \mu\text{mol m}^{-2} \text{s}^{-1}$  on 17/8/82. The overall mean for 5 weeks on the glasshouse bench was highly variable, about  $400 \pm 100 \mu\text{mol m}^{-2} \text{s}^{-1}$ .



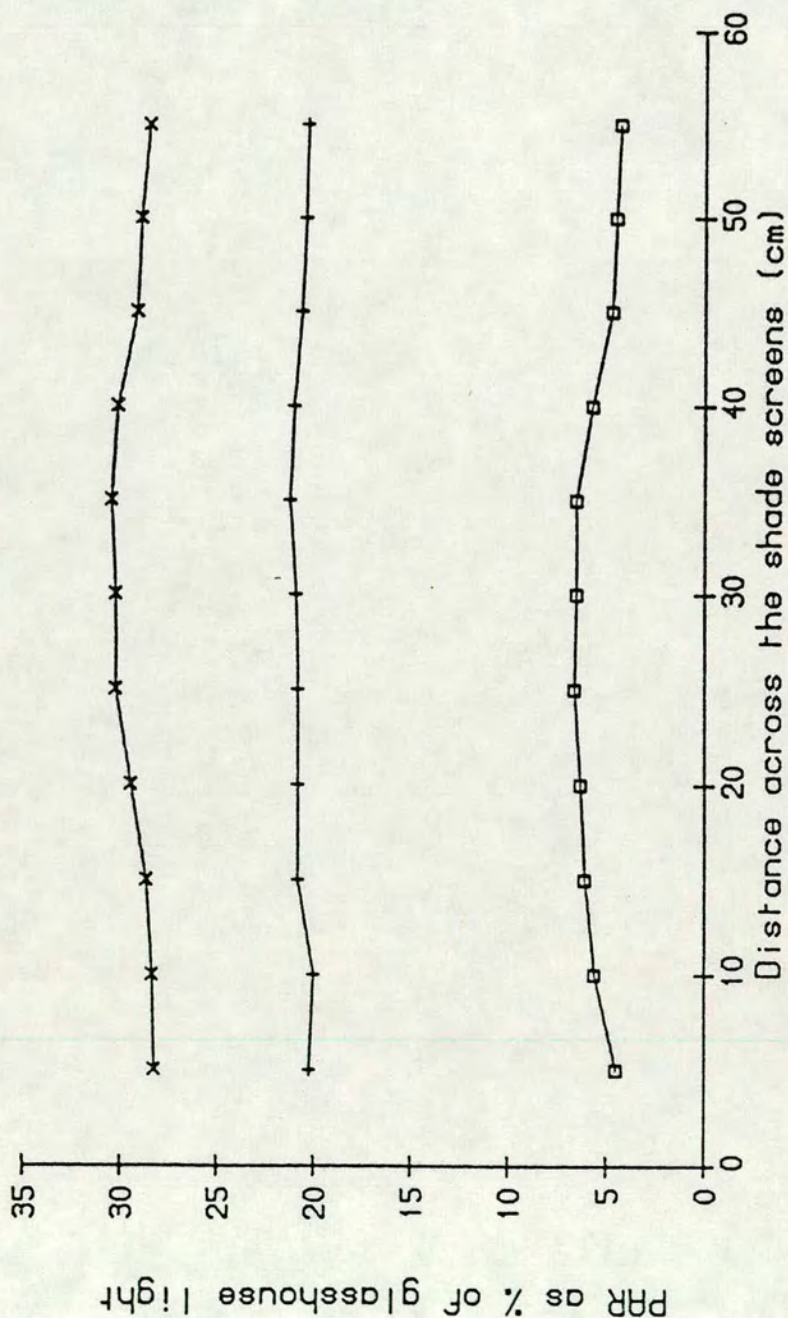


FIGURE 5:1 : Light regime under shade screens recorded on a sunny and hazy day (1/8/82). Typical values of light (PAR) under one layer (x), two layers (+), and three layers of green cinemoid filter material and four layers of muslin (□); in relation to that at the glasshouse bench as described in the text.



#### 5.1.4 Analysis of data

Growth analysis (Evans 1972, Hunt 1978, 1982) is a powerful method for estimating long term net photosynthetic production. It is based on readily obtainable primary measurements of plant dry weight and leaf area made at intervals on growing plants or plant stands. It is also useful for analysing physiological adaptations of different species in terms of their partitioning of carbohydrate into leaves and other organs such as roots, stem or seeds. This partitioning is at least as important as photosynthetic activity per unit area in determining productivity of different plant stands (Jones, 1983). The growth rate or rate of change of total plant dry weight ( $dW/dt$ ) is obtained from a series of destructive harvests. It can be calculated for single plants or for plant stands and either expressed per unit total dry weight as a relative growth rate (RGR) or else expressed per unit ground area as a crop growth rate (CGR). It is possible to derive the net photosynthetic rate per unit leaf area called unit leaf rate or net assimilation rate (NAR). NAR embraces respiratory losses at night and from non photosynthesizing tissues, but it is not quite equivalent to net photosynthesis as measured on single leaves.

At time 1 ( $t_1$ ) on 5/8/82, 15 plants of each species were randomly selected from the 5 height classes. Leaf area (projected) was assessed using the leaf area-meter (LI 3100 Li-Cor, Nebraska). Plant height, number of leaves, and number of abscinded leaves were carefully recorded. The roots were washed of soil on a 2 mm sieve. The other plant organs were separated and dried in the oven at  $90^{\circ}\text{C}$  for 48 hours. Using the Oertling V20 balance, dry weights were recorded.

The fifteen plants harvested on 5/8/82 provided reference values of mean dry weights and leaf area for time  $t_1$ . After 5 weeks of growth, the remaining 60 plants of each species were harvested. There were 5 plants in each of the water treatments corresponding to dry, flooded and field capacity, giving 15 plants in each of the shade



screens and 15 plants in the open as controls.

Statistical analysis was accomplished by making paired comparisons between individual plants of the same initial size class. Hence, within 15 individuals in a size class, 15 independent estimates of RGR and NAR were determined.

### 5.1.5 Calculations

The following calculations are based on Květ *et al* (1971), Evans (1972), and Hunt (1978; 1982).

Relative growth rate (RGR), is defined as the rate of increase in dry weight,  $W$ , per unit dry weight per unit time,  $t$ :

$$RGR = 1/W \cdot dW/dt \quad (5.1)$$

Fisher (1921) pointed out that RGR is most simply expressed as an instantaneous value. But more usefully, mean RGR, from harvest 1 at time  $t_1$  to harvest 2 at time  $t_2$  is obtained by integration between  $t_1$  and  $t_2$ :

$$RGR = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} \frac{1}{W} \cdot \frac{dW}{dt} \cdot dt = \frac{(\ln W_2 - \ln W_1)}{t_2 - t_1} \quad (5.2)$$

Where  $W_1$  and  $W_2$  are mean total dry weights at times  $t_1$  and  $t_2$  and the units of RGR are  $\text{time}^{-1}$  (e.g.  $\text{g g}^{-1} \text{ week}^{-1} = \text{week}^{-1}$ ).

Net assimilation rate (NAR), is the rate of increase in dry weight per unit of leaf area ( $A$ ), per unit time; which is an estimate of the carbon-assimilatory capacity of the leaves:

$$NAR = \frac{1}{A} \cdot \frac{dW}{dt} \quad (5.3)$$



NAR is also an instantaneous value.  $A$  is the total leaf area present on the plant. Williams (1946) provided a convenient formula for estimating mean NAR over a period of time. Assuming  $A$  is linearly related to  $W$ , (e.g. Blackman 1968; Ondok 1971a); NAR is ;

$$\text{NAR} = \frac{W_2 - W_1}{t_2 - t_1} \cdot \frac{\ln A_2 - \ln A_1}{A_2 - A_1} \quad (5.4)$$

Where  $W_1$  and  $W_2$  are mean total dry weights and  $A_1$  and  $A_2$  are mean total leaf area at times  $t_1$  and  $t_2$ . Units of NAR are weight per area per time (e.g.  $\text{g m}^{-2} \text{ week}^{-1}$ ).

Leaf area ratio (LAR) is the ratio of leaf area to total plant weight. In a broad sense, LAR represents the ratio of photosynthesizing to respiring material within the plant (Hunt 1982).

$$\text{LAR} = \frac{A}{W} \quad (5.5)$$

over a harvest interval, its mean value is simply given by

$$\text{LAR} = \frac{(A_1/W_1) + (A_2/W_2)}{2} \quad (5.6)$$

Radford (1967) showed that a mean value for LAR cannot be satisfactorily determined, so the final harvest values of  $A$  and  $W$  were used in this and other experiments to estimate LAR. Units of LAR are area per weight (e.g.  $\text{m}^2 \text{ g}^{-1}$ ).

From equations 5.1, 5.3 and 5.5; it can be seen that instantaneously;

$$\text{RGR} = \text{NAR} \cdot \text{LAR} \quad (5.7)$$



A change in RGR must be reflected in either NAR or LAR.

LAR may be divided into leaf weight ratio (LWR) and specific leaf area (SLA). LWR is the ratio of leaf weight ( $W_1$ ) to total dry weight:

$$LWR = \frac{W_1}{W} \quad (5.8)$$

LWR is a dimensionless index of the leafiness of the plant on a weight basis. SLA is the mean area of leaf displayed per unit of leaf dry weight ( $W_1$ ):

$$SLA = \frac{A}{W_1} \quad (5.9)$$

The units of SLA are area per weight (e.g.  $m^2 g^{-1}$ ). In a sense it is a measure of leaf density or relative thickness (Hunt, 1982).

$$\text{Thus, } LAR = SLA \cdot LWR \quad (5.10)$$

of these two subdivisions of LAR, SLA is in general the more sensitive to environmental changes and more prone to ontogenetic drift. Thus a change in LAR must be reflected in SLA or LWR.

#### 5.1.6 Statistical package : GENSTAT

Genstat is a computer program designed to help analysis of data and is used extensively in agronomy, animal husbandry genetics, ecology, medical research and other areas of biology (Alvey et al., 1982). It is used in this thesis especially in the analysis of variance (ANOVA) within treatments and between species for purposes of tests of significance and confidence limits (Parker 1979).



Using a two sided t-statistic:

$$t = \frac{\text{mean}_1 - \text{mean}_2}{\text{(standard error of difference)}} \quad (5.11)$$

it is possible to estimate the least significant difference (LSD) between specific means, by multiplying the standard error of difference between two means (SED) by t for n degrees of freedom. Thus, a specific treatment mean was declared significant at 95 % probability level if  $\pm\text{LSD}$  was exceeded. For details of the method refer to Snedecor and Cochran (1967), and Sokal and Rohlf (1969, p. 226-235).

## 5.2 Results

The transmittance of No. 22 'Mossgreen' cinemoid filter was particularly low in the red relative to the far-red (Table 5.1). The calculated R/FR for 1, 2 and 3 layers of filter material was 0.356, 0.106 and 0.031 respectively (Table 5.2). The addition of muslin and glasshouse walls did not affect the R/FR much, as those materials were optically neutral (Table 5.3).

There was a slight fall off in PAR near the edges of the shade screens (Fig. 5.1). However, a range of shade was achieved. In a series of measurements conducted when there was a hazy sky the range from full glasshouse light on the open bench to only 5 % in the shade of 3 layers of filter plus 4 layers of muslin was common (Fig. 5.1). On sunny days near noon, the values were slightly higher than this on a weekly average. Differences observed between days can be attributed to variation in radiation geometry and prevailing weather conditions at the time of the year.



TABLE 5.1: Transmittance of cinemoid filters at 660 and 730 nm.

FILTER	TRANSMITTANCE	TRANSMITTANCE	RED/FAR-RED
	IN RED (660 nm)	IN FAR-RED (730 nm)	TRANSMITTANCE RATIO
No. 21	0.304	0.648	0.469
No. 22 (Mossgreen)	0.088	0.296	0.297
No. 23	0.141	0.380	0.371
No. 24	0.044	0.111	0.396
No. 38	0.733	0.944	0.776
No. 39	0.043	0.111	0.387
No. 77	0.755	0.944	0.799
BBC GREEN	0.088	0.222	0.396

TABLE 5.2 : Calculated R/FR ratio under different layers of filter material based on the open value of full sunlight. (R/FR $\approx$ 1.2) as given by Smith (1982).

FILTER	1 LAYER	2 LAYERS	3 LAYERS
NO. 21	0.563	0.260	0.120
No. 22 (Mossgreen)	0.356	0.106	0.031
No. 23	0.445	0.165	0.006
No. 24	0.475	0.187	0.077
No. 38	0.931	0.717	0.556
No. 39	0.464	0.216	0.046
No. 77	0.959	0.760	0.614
BBC GREEN	0.473	0.187	0.074



TABLE 5.3 : Transmittance of Muslin and Whitewashed glasshouse glass.

	1 LAYER OF MUSLIN	2 LAYERS OF MUSLIN	GLASS(Whitewashed)
Red (660 nm)	0.76	0.62	0.775
Far-red (730 nm)	0.792	0.65	0.775
R/FR ratio	0.96	0.95	1.0

### 5.2.1 Growth analysis

The main results of analysis of variance have been summarized in Table 5.4. It is also shown that water status treatments had significant effects only on root growth in both species and slight effects on leaf and stem growth in *Khaya senegalensis*. Consequently, all the treatments have been pooled in order to discuss the effects of shade.



TABLE 5.4 : Main results of Analysis of Variance

(Not significant = ns; \* $P < 0.1$ ; \*\* $P < 0.05$ ; \*\*\* $P < 0.01$ ; \*\*\*\* $P < 0.001$ ).

Species 1 = *Terminalia ivorensis*

Species 2 = *Khaya senegalensis*

SPECIES	VARIATE	FACTORS:		Water-shade interaction
		Water	Shade	
1	Leaf abscission	ns	**	ns
2		ns	ns	ns
1	Ln Leaf area	ns	*****	ns
2		ns	ns	ns
1	Root dry weight	**	*****	*
2		***	*****	***
1	Root/shoot ratio	ns	ns	ns
2		*****	***	ns
1	Leaf area ratio	ns	*****	ns
2		ns	*****	ns
1	Specific leaf area	ns	*****	ns
2		ns	ns	ns
1	Leaf weight ratio	ns	***	ns
2		**	****	ns
1	Stem height ratio	ns	*****	ns
2		ns	*****	ns
1	Relative growth rate	ns	*****	ns
2		ns	*****	ns
1	Net assimilation rate	ns	*****	ns
2		ns	*****	ns



### 5.2.2 Effects of shade

The following were shown by analysis of variance (Table 5.4) to be significant shade effects:

1) Shade induced leaf abscission in *Terminalia ivorensis*, but not in *Khaya senegalensis* (Table 5.4). It was mainly by this means that shade significantly affected final leaf area: it was reduced under various levels of shading in *Terminalia*. On the other hand *Khaya* neither produced nor lost any leaves. Instead it simply set a dormant bud.

2) After a period of growth in shade both species displayed more stem height per unit plant weight than in the open (Fig.5.2).

3) The effects of shade, water levels and their interactions had significant effects on root growth (Fig. 5.3a and 5.3b), with a significant decrease in root/shoot ratio with increasing shade in *Khaya senegalensis* alone (Table 5.4).

4) In *T. ivorensis*, final LAR was lower in the open compared to all levels of shading; and the final SLA was significantly higher in shaded plants than those grown in the open glasshouse conditions (Fig. 5.4a). In *Khaya senegalensis*, LAR was also higher in shaded plants but SLA was hardly affected (Fig. 5.4b, Table 5.4). As a result of shade induced increases in LAR and SLA in *Terminalia ivorensis*, LWR was affected by shade and it was maximal with one shade screen, but declined in deeper shade (Fig. 5.5a); shade also affected LWR in *Khaya senegalensis* (Fig. 5.5b).

5) Under shade, the NAR of *Terminalia ivorensis* became negative (Fig. 5.6a) and the RGR was also negative (Fig. 5.7a). In contrast, *Khaya senegalensis* achieved a positive NAR (Fig. 5.6b) and a positive RGR (Fig. 5.7b) at all the levels of PAR.

In conclusion, ~~decreases~~ in relative growth rate are caused by a reduction in net assimilation rate despite some compensation via an increase in leaf area ratio. This increase in leaf area ratio was



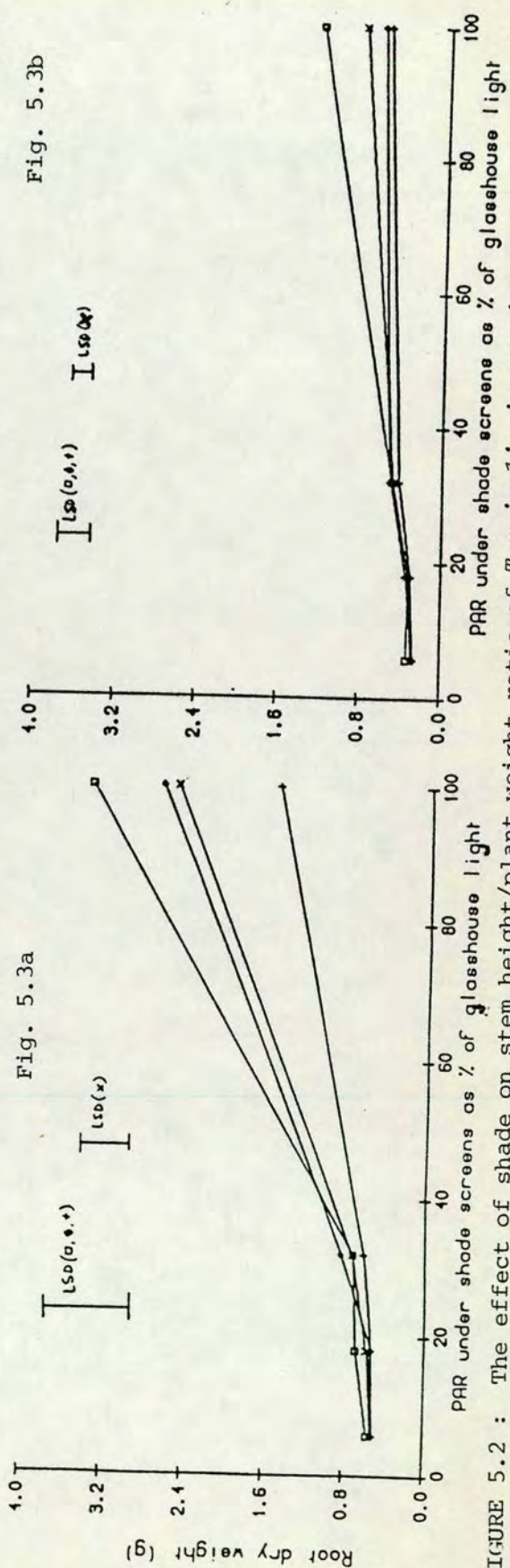
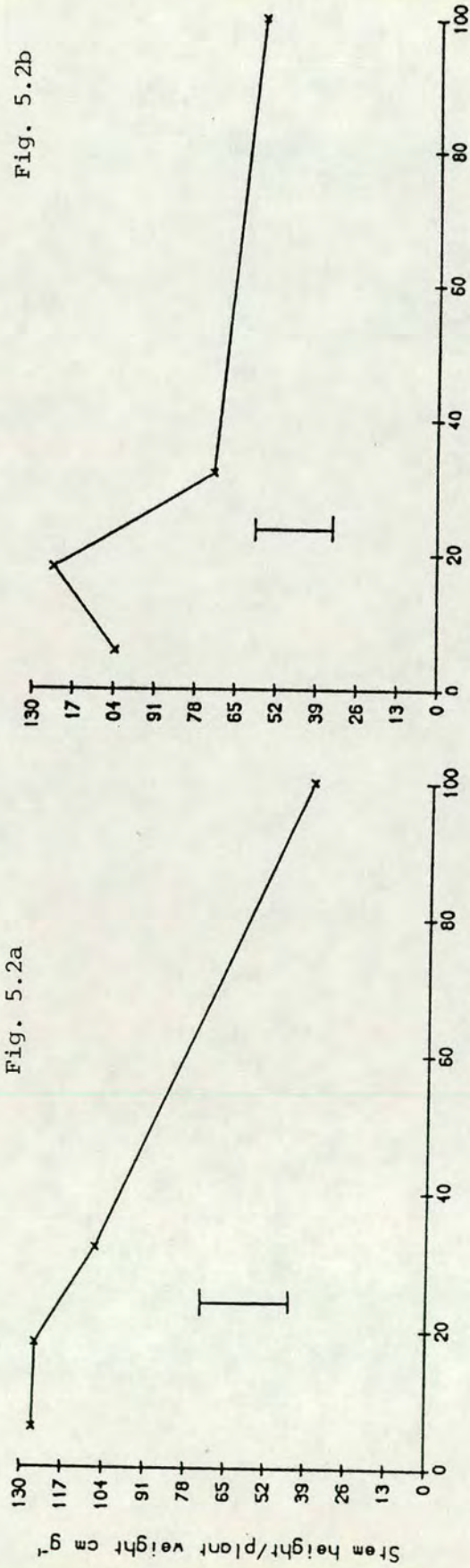


FIGURE 5.2 : The effect of shade and water interaction on root growth as described in the text: (□) plants at field capacity, (x) overall effect of shade, (◆) plants subjected to drought conditions, (+) plants subjected to flooding

FIGURE 5.3 : The effect of shade and water interaction on root growth as described in the text: (□) plants at field capacity, (x) overall effect of shade, (◆) plants subjected to drought conditions, (+) plants subjected to flooding

(a) *Terminalia ivorensis* (b) *Khaya senegalensis*. The bars represent LSD at 95 % (see Table 5.4).



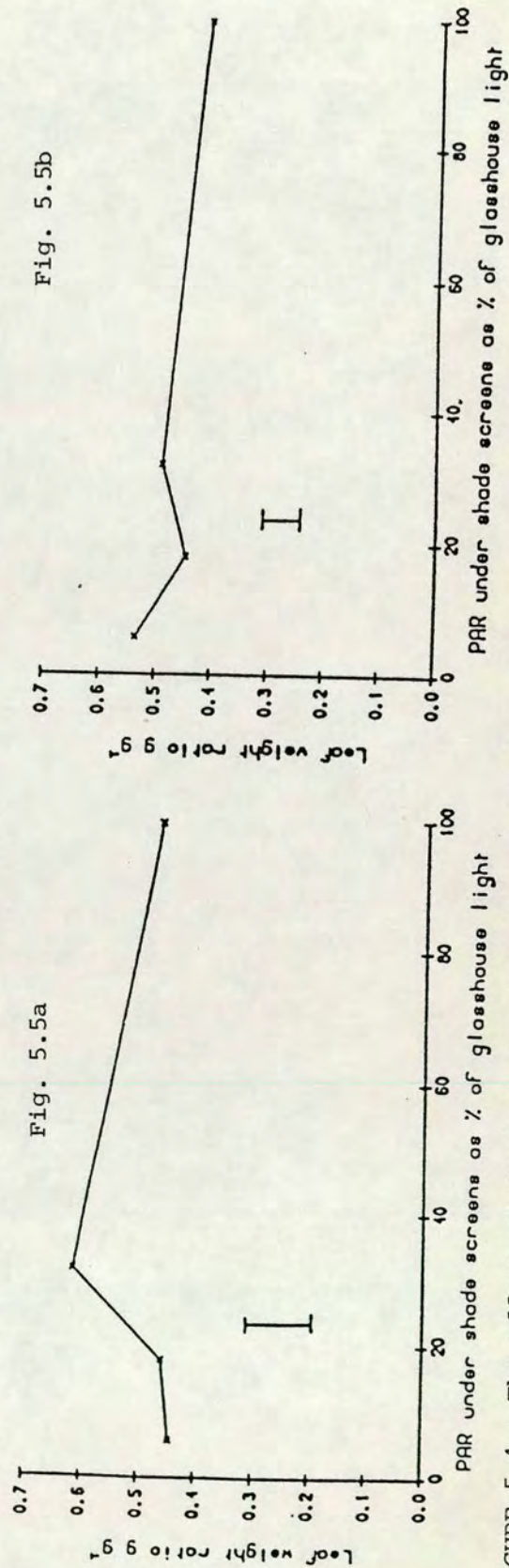
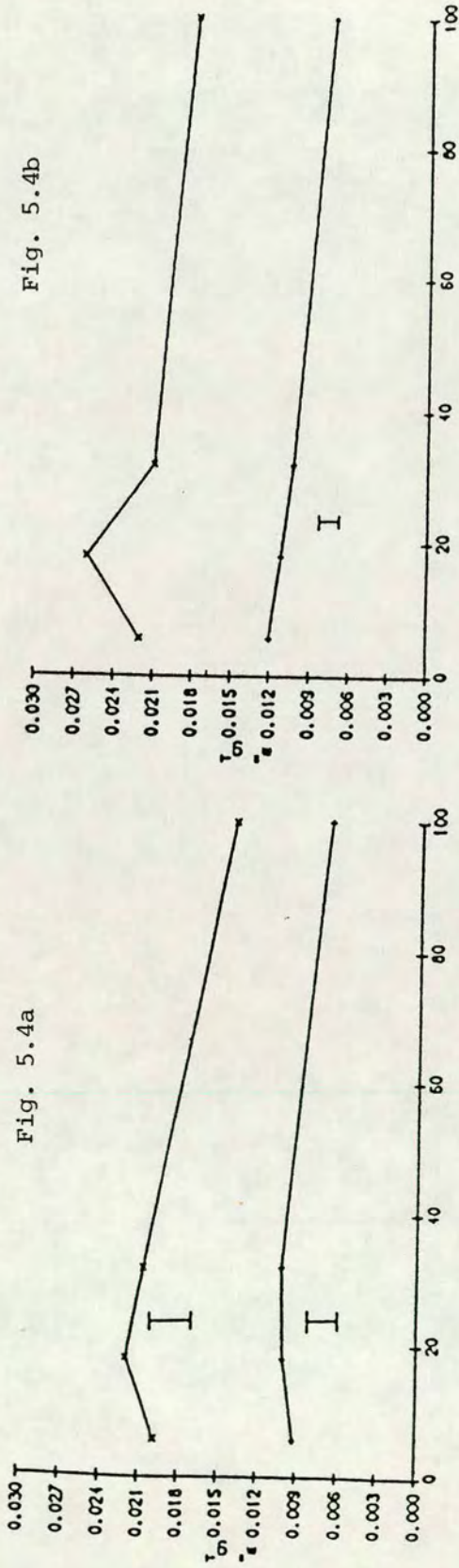


FIGURE 5.4 : The effect of shade on final leaf area ratio (x) and specific leaf area (+) on *Terminalia ivorensis* (a) and *Khaya senegalensis* (b) units  $\text{m}^2 \text{g}^{-1}$ .

FIGURE 5.5 : Effect of shade on final leaf weight ratio in *Terminalia ivorensis* (a) and *Khaya senegalensis* (b). The bars represent LSD at 95 % (see Table 5.4).



Fig. 5.6a

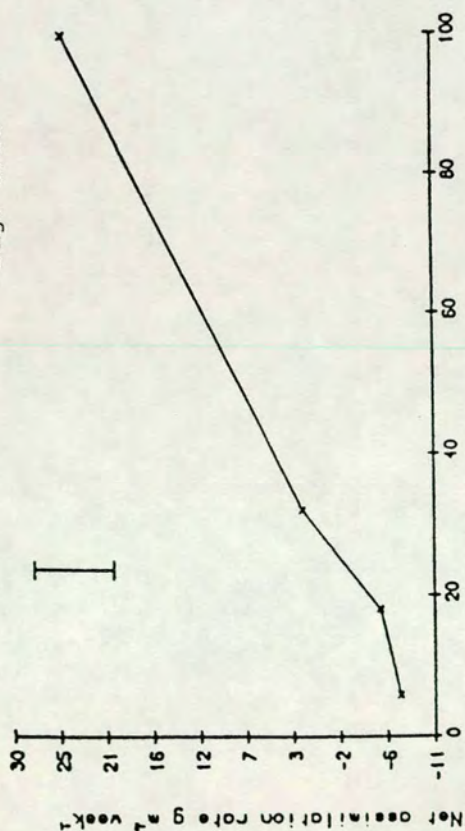


Fig. 5.6b

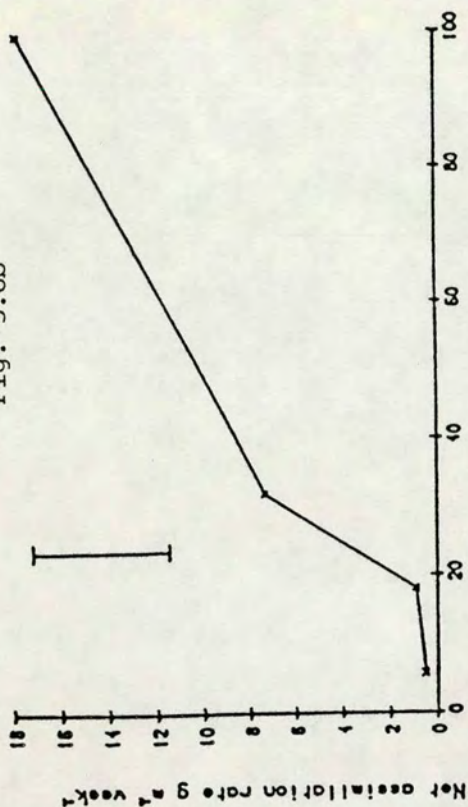


Fig. 5.7a

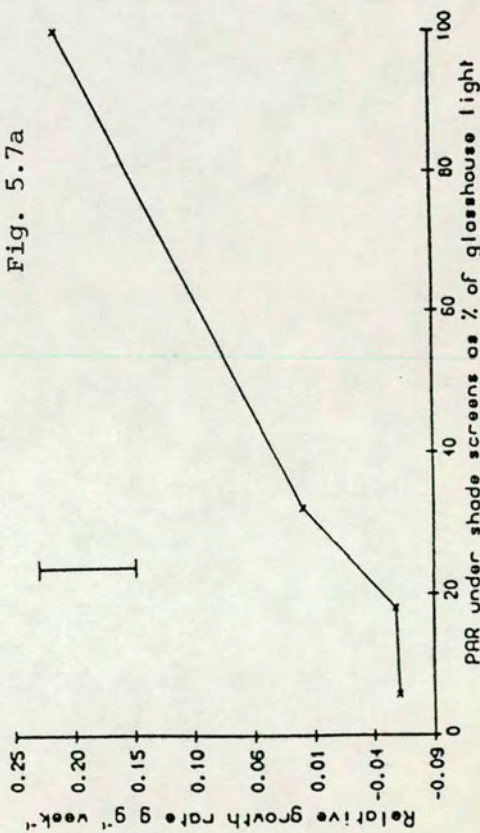


Fig. 5.7b

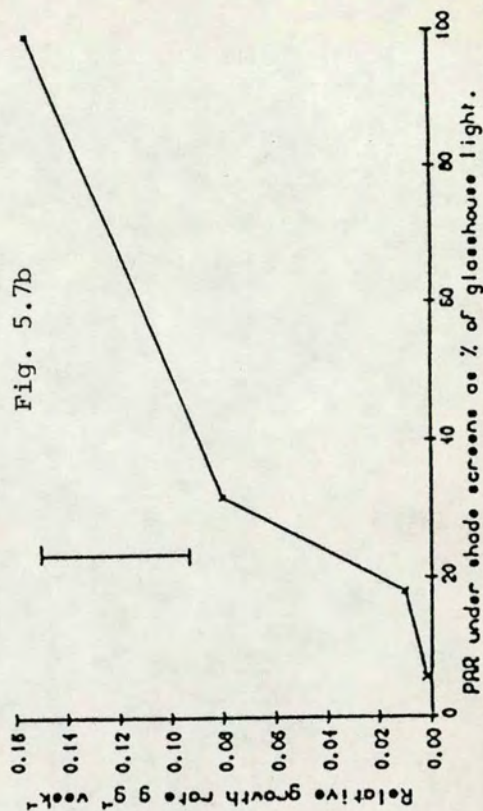


FIGURE 5.6 and 5.7 : The effect of shade on net assimilation rate (Fig. 5.6) and relative growth rate (Fig. 5.7) on *Terminalia ivorensis* (a) and *Khaya senegalensis* (b). Note that the scales are not the same for both species. The bars represent LSD at 95 % (see Table 5.4). Units: Net assimilation rate (g m<sup>-2</sup> week<sup>-1</sup>) and relative growth rate (g g<sup>-1</sup> week<sup>-1</sup>).



accomplished in *Terminalia* by an increase in specific leaf area. *Khaya* remained in a positive carbon balance even in the deepest shade but *Terminalia* did not.

### 5.3 Discussion

#### 5.3.1 Evaluation of Experimental conditions

Levels of PAR were achieved which were as low as those expected at the forest floor. However, the 'open' levels were not very high, and certainly not as high as the open tropical conditions. Also the photoperiod, of about 14 hours, was longer than tropical conditions.

Temperature in the glasshouse was adequately high as experimentation was restricted to summer months.

Water levels had only weak effects, probably because the experiment was not continued for sufficiently long.

#### 5.3.2 Response to shade

In deep shade the light demander *Terminalia ivorensis* was below its light compensation point NAR and RGR being negative. It lost its leaves and did not make a dormant bud. On the other hand, the shade tolerator *Khaya senegalensis* did not fall below light compensation point, did not lose any leaves and its bud became dormant.

Since *Khaya* increased in weight but did not produce new leaves or any extension of the stem, it presumably stored the products of photosynthesis in the stem and leaves. Also, there were differences in leaf morphology. *T. ivorensis* developed thinner leaves with a significantly higher SLA, but this was not the case in *Khaya senegalensis* although both species showed a similar trend in LAR response to shade.

The results of this experiment suggest that there are differences in response to shade between these two species. This is



viewed as indicative of differences in adaptation to survival in an intermittent light regime that is characteristic of the forest floor. *Khaya senegalensis* shows an advantage under shade: it can survive in dense shade and even increase in weight. Then when a canopy gap occurs, growth may presumably be achieved at the expense of storage products, like temperate trees after winter. The negative RGR and NAR in *Terminalia ivorensis* indicate the respiration rates may be higher in shade for light demanders; this topic will be returned to in a later chapter.

In conclusion, it seems from these preliminary experiments that the two species do indeed respond differently to simulated shade, and that their responses may be interpreted as adaptive and to a large extent similar to those reported for tropical and temperate trees elsewhere (Coombe 1960; Coombe and Hadfield 1962; Jarvis and Jarvis 1964; Okali 1971, 1972; Synnott 1975; Fasehun and Audu 1980). The influence of water regimes was subsidiary and secondary to the response to shade, at least in these short term experiments, and consistent with the grosser responses to drought and flooding reported elsewhere (Levitt 1980, Crawford 1982).

It was decided henceforth to concentrate on further analysis of response to shade: in particular, to use a controlled environment to facilitate the use of very high levels of PAR; and to attempt to separate the roles of reduced PAR *per se* and reduced R/FR ratio.

It was also decided that these two species would be suitable subject for study. They behave in a contrasting manner, their seed was available and cultivation of them presents no great difficulties.



## CHAPTER SIX

### *THE ROLE OF THE RED/FAR-RED RATIO IN THE RESPONSE OF SEEDLINGS TO SHADE*

#### 6.1 Introduction

In the preliminary experiment (Chapter 5), no attempt was made to separate the effects of a reduced photon flux density from those of a reduction in the R/FR ratio. In common with most investigations on the effects of shading on plant growth, it was assumed that shading was synonymous with a decreased photon flux density: the changes in the spectral distribution that occur in natural shade and their effects were not investigated. However, advances in techniques of simulating natural light spectra within controlled environments have meant that extensive research on the physiological and ecological significance of spectral quality has recently become possible. A review on this subject is presented in Section 3.3 (see also Morgan and Smith 1981, Smith 1982).

In this chapter, an attempt has been made to separate the effects of reduced photon flux density and R/FR ratio, varying them over a range which, as far as possible, is typical of natural light climates. In this way, as will be reported later, it was possible to characterize the observed effects on growth response of two contrasting species.

Photon flux densities of 18, 125, 250 and 610  $\mu\text{mol m}^{-2} \text{s}^{-1}$  were obtained using cinemoid filters and neutral muslin whilst the R/FR ratios were in the range 0.14 to 1.7. Thus, it was possible to separate the effects of a reduced photon flux density from those of R/FR as the muslin material has almost no effect on R/FR ratio, acting as a neutral filter. The green cinemoid filter, however, markedly affects the R/FR ratios.



The experiment was carried out in a Fisons growth cabinet where temperature and humidity were controlled to obtain tropical conditions as far as possible.

## 6.2 Materials and Methods

The materials and methods employed in this experiment were as far as possible similar to those reported in Chapter 5, except that very young seedlings were used and the experiment was carried out in the growth cabinet.

Cinemoid filter mossgreen No. 22 (Northern Lights, Edinburgh), muslin and perforated hardboard were used to vary photon flux density and red/far-red ratios. They were tested in the Fisons growth cabinet (Type 2340, Loughborough, U.K.) using a Quantum spectroradiometer (QSM-2500, Techum Instruments, Sweden).

Quantum flux densities associated with each wavelength were measured by scanning across the 400-750 nm waveband. A quantum sensor on the Li-Cor porometer (LI-1600 Li-Cor, Nebraska) was also used to measure overall photon flux density in the photosynthetically active waveband (400-700 nm).

After several trials photon flux densities and R/FR ratios under cinemoid filters and several layers of muslin were established. Initially, photon flux density and red/far-red ratio under green cinemoid filters was established. Then, the corresponding photon flux density under neutral muslin material was obtained using several layers of muslin to match that under the cinemoid filters. Afterwards the red/far-red ratio was measured.

Photon flux densities and R/FR ratios under the cinemoid filters and muslin were matched as shown in Table 6.1.



TABLE 6.1: Shade screens and the light climate they produce

TREATMENT DESCRIPTION	PAR( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	RED/FAR-RED RATIO (R/FR)
Open* (32 cm from light chamber)	610	1.70 $\pm$ 0.14
1 layer of mossgreen cinemoid filter	250	0.596 $\pm$ 0.06
4 layers of muslin	250	1.66 $\pm$ 0.04
2 layers of mossgreen cinemoid filter	125	0.282 $\pm$ 0.03
8 layers of muslin	125	1.70 $\pm$ 0.03
3 layers of cinemoid and 4 layers of muslin	18	0.141 $\pm$ 0.019
2 layers of muslin and one perforated hardboard	18	1.64 $\pm$ 0.02

\*Details of growth cabinet are presented in chapter seven.

### 6.2.1 Wooden frames

Two wooden frames which could fit into the growth cabinet were constructed. Each frame consisted of four compartments on which either cinemoid filters or muslin were mounted using staples. Details of one of two identical frames are shown in Fig. 6.1

Each compartment was separated by a sliding hardboard shutter covered with a thin layer of reflective Melinex (ICI) on both sides. The reason for Melinex on both sides was to eliminate stray light and hence to eliminate edge effect. In Fig. 6.1, the hardboard with reflective Melinex is hatched. Each frame had such boundaries of compartments with hardboard held in suspension by adjustable nails.

The seedlings were raised in plastic pots 9 cm high by 9.5 cm diameter. Each of the compartments (46 cm x 48 cm x 36 cm) could accommodate 20 such pots, effectively 10 plants of each species.



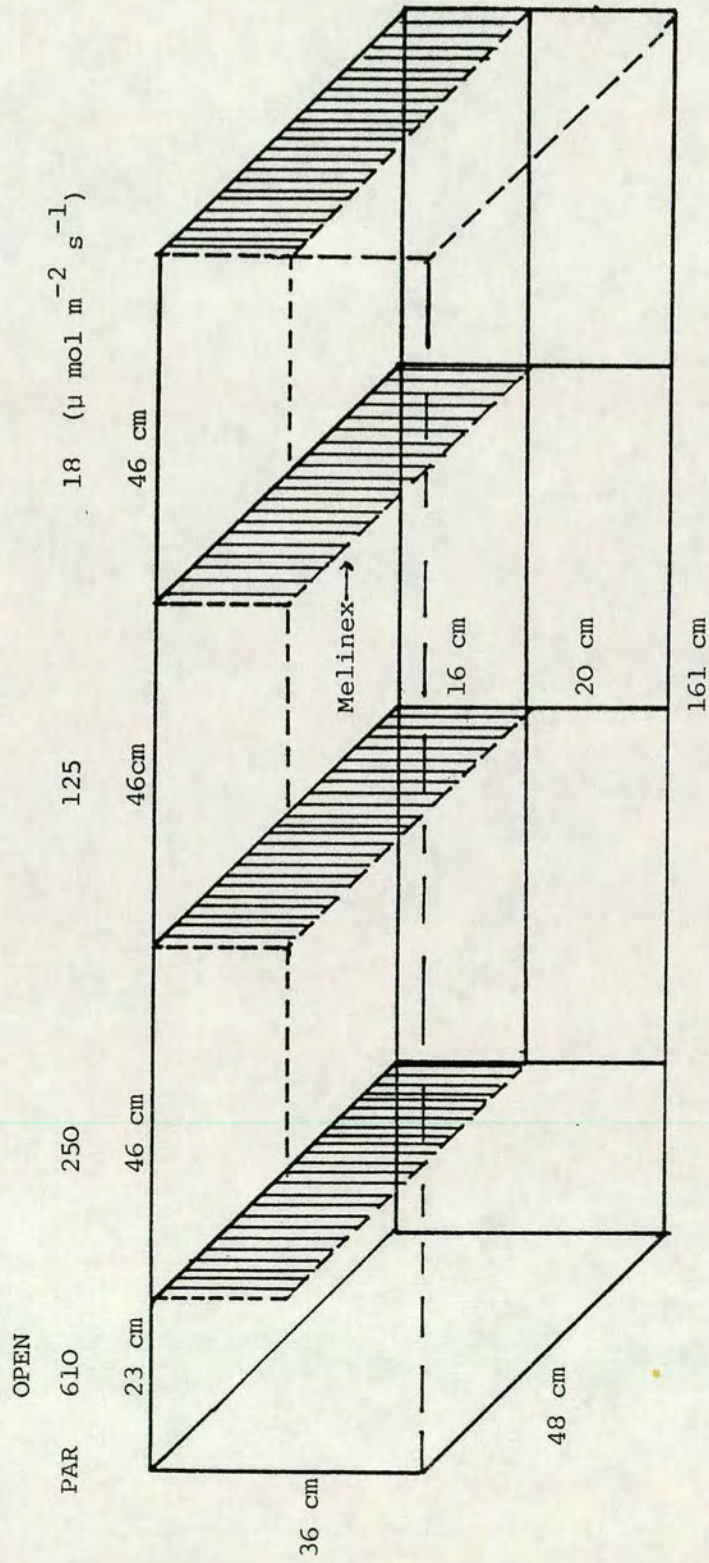


FIGURE 6.1: Dimensions and layout of one of the two identical wooden frames under which the plants were raised in the Fisons growth cabinet as explained in the text. The sliding hardboard shutter covered with reflective melinex is hatched.



To eliminate further interference at the boundary zone, all the plants were raised higher up by empty pots of 9 cm x 9.5 cm diameter in an inverted position so that most of the plants' growing points were under the desired treatment conditions. On average, *Khaya senegalensis* seedlings were about 9 cm tall and *Terminalia ivorensis* 4 cm tall at the time of transfer to the growth cabinet.

The frames were arranged side by side and were separated from the cabinet wall at the back side by a 2 cm gap to allow adequate air circulation.

Air flow in the cabinet is laminar and from right to left (for full details refer to Section 7.2.2). The plants in open treatment were adjacent to the zone of highest air flow on the left hand side of the cabinet in anticipation of increased leaf temperature due to a higher photon flux density in the open condition. In order to increase further the circulation in the compartments, the lower half of the right hand side of the cabinet was blocked with hardboard 91 cm x 50 cm.

#### 6.2.2 Red/far-red ratios (R/FR)

The red/far-red ratios were measured by scanning across the 400-750 nm waveband using a spectroradiometer and a chart recorder. Quantum flux densities at all wavelengths were recorded and from readings at 660 nm and 730 nm the R/FR ratio was calculated (Table 6.1, Fig. 6.2).

In order to assess if there were any differences at different locations of the compartments, 9 values of R/FR were calculated from readings taken on a 3 x 3 regular sampling matrix. The average was taken as representative of each compartment's quantum flux.

On each of the sample points, the spectroradiometer sensor head was raised 60 mm and 105 mm respectively, to assess the effect of variation of plant height which might occur during the experiment.



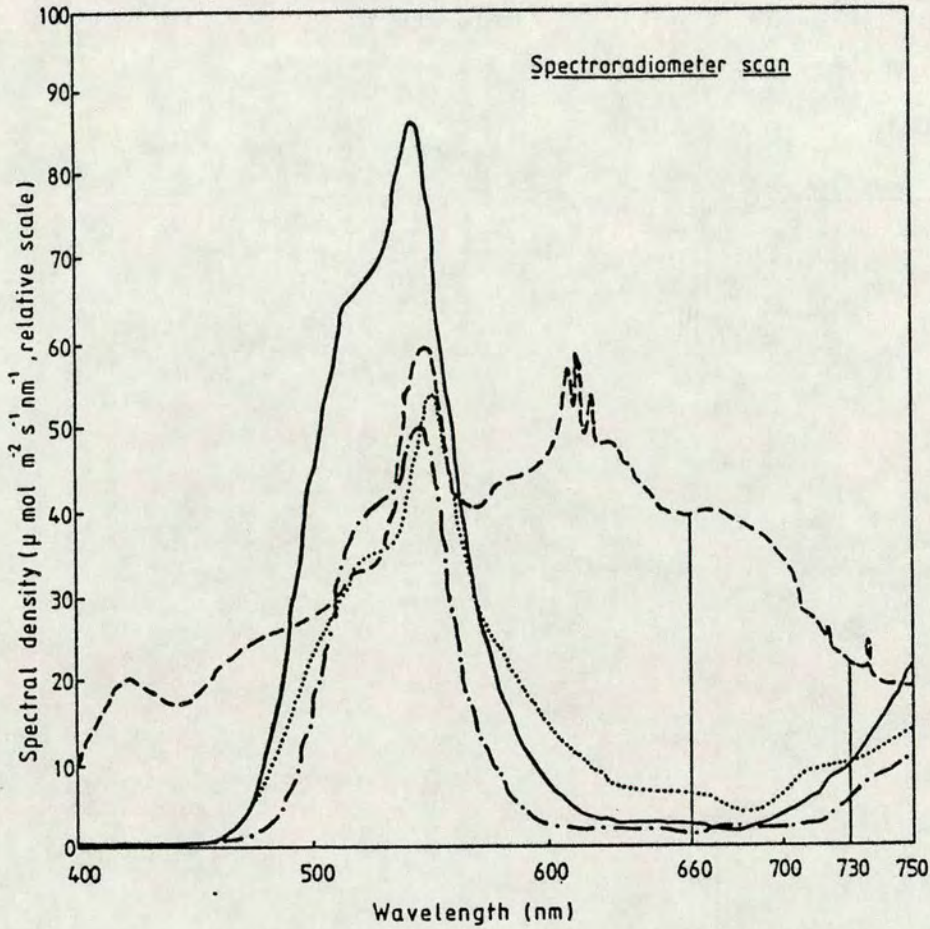


FIGURE 6.2 : Spectroradiometer scans in the Fisons cabinet under the shade screens (Fig. 6.1). The red/far red ratio was measured as described in the text. Details of PAR and R/FR are presented in Table 6.1.

- open conditions in the Fisons cabinet
- one layer of cinemoid filter material 30 times the sensitivity
- ..... two layers of filter material
- 3 layers of muslin and hardboard



### 6.2.3 Photon flux density

Photon flux density was measured by a quantum sensor (Li-Cor, Nebraska). Initially the cinemoid filters were mounted on the wooden frames (Section 6.2.1). Photon flux densities under one layer, two layers, and three layers plus four layers of muslin were measured. Then the corresponding values under neutral filters were matched (Table 6.1).

### 6.2.4 Plant material

Seeds of Nigerian provenance, of the same batch as in the preliminary experiment (Chapter 5) were used. Two hundred seeds of each species were sown in sand under the mist bench conditions in the glasshouse. They were sown on 14/7/83. After two days, they were covered with a white polythene sheet. By the end of two weeks, germination was complete and suitably high.

On 28/7/83, 80 seedlings of each species were transplanted in a UC 50:50 Sphagnum peat and sand mixture of pH 5.5. On 5/8/83, 10 seedlings of each species were selected at random and harvested. At the time, *Khaya senegalensis* had one pair of simple leaves whilst *Terminalia ivorensis* had a pair of cotyledonary leaves and a very young pair of true leaves. The other 70 seedlings of each species were transferred to the Fisons growth cabinet.

Under each of the treatment conditions described in Section 6.2 (Table 6.1), there were 10 seedlings of each species distributed randomly in each compartment. These seedlings were grown for 5 weeks under conditions reported in Section 7.2.2

### 6.2.5 Watering

A twenty litre plastic container with a tap at the bottom was used as water reservoir. This was put about 1 metre above the growth cabinet level on a steel structure outside the growth cabinet. With a system of plastic tubing, it was easy to connect a five metres long tube to the tap and consequently water the plants without having



to remove the shade screens. Watering was at least once a day.

### 6.2.6 Analysis of data and calculations

The methods presented in Chapter 5, Sections 5.1.5 and 5.1.6 were followed. Least significant difference (LSD) was used where F was significant. F was computed as shown in Table 6.2.

TABLE 6.2: Computation of F.

SOURCE OF VARIATION	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARES	F
Treatments	SST	k-1	MST = SST/k-1	MST/MSE
Error	SSE	k(n-1)	MSE = SSE/k(n-1)	-
(TOTAL)	(SS)	(kn-1)	-	-

If the computed value is equal to or exceeds the tabulated value for  $P=0.05$  we normally reject the null hypothesis and conclude that the samples represent populations with different means, in other words, there are significant differences between treatment means. In *a priori* comparisons (such as in these experiments) the method of LSD was employed as reported in Sections 5.1.5 and 6.

$LSD = t_{0.05} \sqrt{(2S^2/n)}$ , where  $t$  has  $k(n-1)$  degrees of freedom (See Parker 1979 pp. 68-90).



### 6.3 Results

Tables 6.3 and 6.4 show raw data obtained by harvesting the plants after 5 weeks of growth on 9/9/83. The leaf area and dry weight data were used to obtain the mean relative growth rate (RGR), net assimilation rate (NAR) and the final leaf area ratio (LAR).

#### 6.3.1 Relative growth rate

Fig. 6.3a shows the mean RGR ( $\text{week}^{-1}$ ) for *Terminalia ivorensis* and Fig. 6.3b for *Khaya senegalensis*, grown at high and low R/FR under a corresponding PAR. The main effects of these treatments were:

- 1) *Terminalia ivorensis* showed a higher RGR than *Khaya senegalensis*
- 2) When *Terminalia ivorensis* was subjected to a low R/FR (Fig. 6.3a) it again responded by a higher RGR than *Khaya senegalensis* (Fig. 6.3b), RGR rose to an asymptote of around  $0.6\text{--}0.7 \text{ week}^{-1}$ . Thus *Terminalia ivorensis* displayed higher rates of growth when R/FR was low. When the R/FR was high, the species did not differ in RGR.

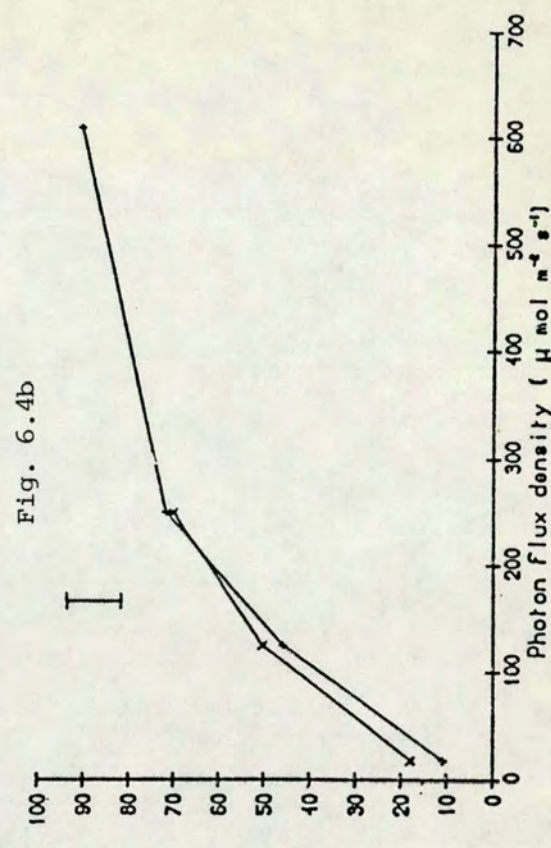
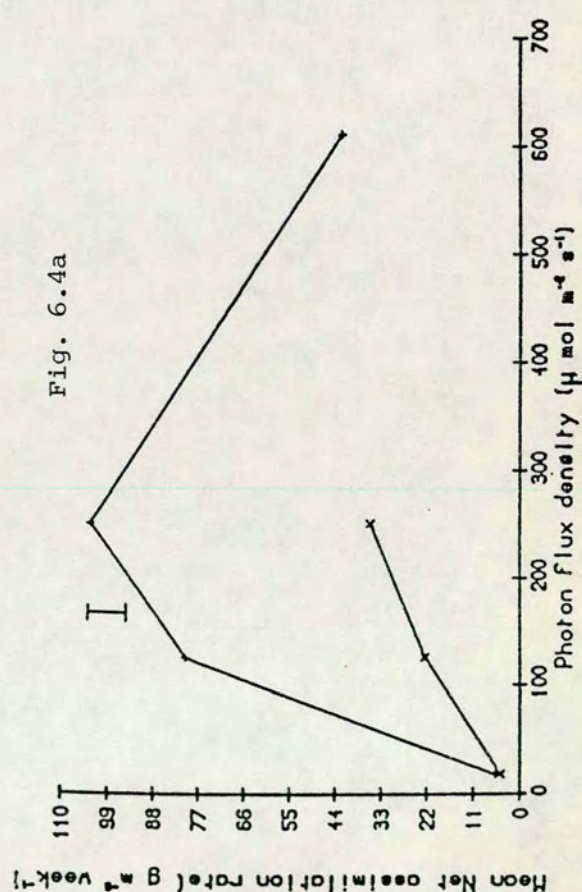
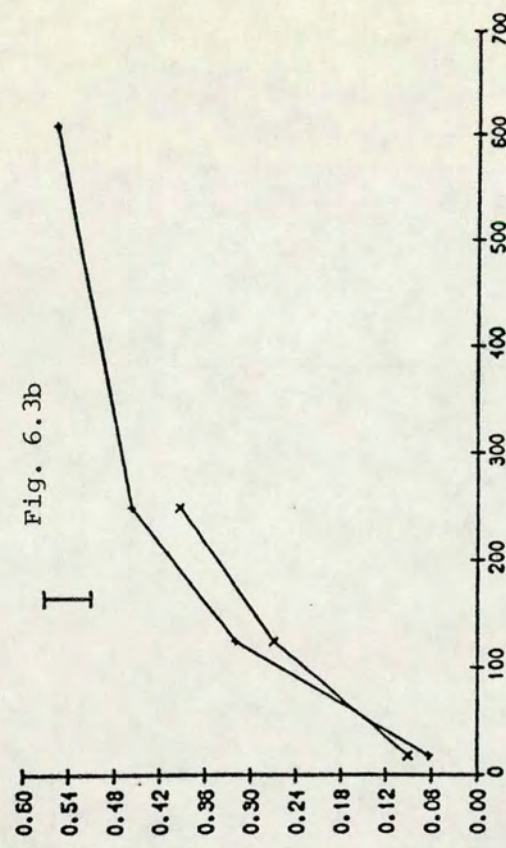
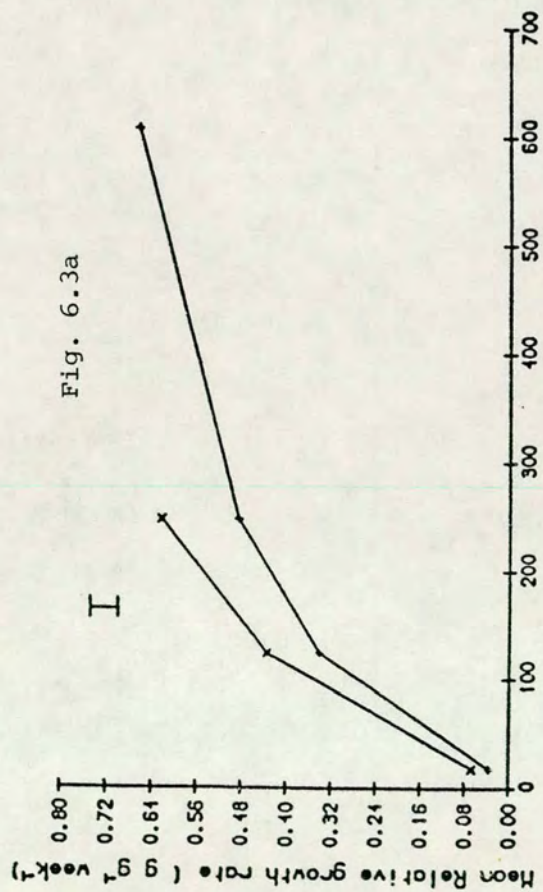
#### 6.3.2 Net assimilation rate (NAR), Leaf area ratio (LAR) and Specific leaf area (SLA)

To understand the causes of differences in RGR, it is important to relate RGR to NAR and LAR. Fig. 6.4a shows NAR ( $\text{g m}^{-2} \text{ week}^{-1}$ ) for *Terminalia ivorensis* and Fig. 6.4b shows the mean NAR for *Khaya senegalensis* attained under the experimental conditions for 5 weeks.

Inspection of Figs. 6.3 and 6.4 shows that the range of photon flux densities under experimental conditions included light saturation around  $600 \mu\text{mol m}^{-2} \text{ s}^{-1}$ .

*Terminalia ivorensis* showed a higher NAR under high R/FR (Fig. 6.4a) than under low R/FR with a corresponding PAR. *Khaya senegalensis* (Fig. 6.4b) did not show significant differences in NAR as a result of growth at low or high R/FR under corresponding PAR.





FIGURES 6.3 and 6.4: The effect of growth at low (x) and high (+) R/FR ratio on relative growth rate (Fig. 6.3) and net assimilation rate (Fig. 6.4) in *Terminalia ivorensis* (a) and *Khaya senegalensis*. (b).



TABLE 6.3

PAR ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ )	18	125	250	18	125	250	610	LSD at 95 %
RED/FAR-RED (R/FR) RATIO	0.14	0.28	0.59	1.64	1.70	1.66	1.70	
Mean number of leaves	6.9	12.1	15.1	7.4	10.8	13.1	15.9	0.96
Mean number of Internodes	3.8	8.4	10.6	3.6	7.4	9.7	11.8	0.95
Mean Internode length (mm)	6.4	12.3	12.6	5.2	11.7	11.3	10.0	1.80
Mean Stem height (cm)	5.8	13.8	17.3	5.5	12.5	14.9	14.9	2.07
Mean Leaf area ( $\text{cm}^2$ )	5.9	54.7	115.9	0.7	2.5	8.0	130.7	19.3
<u>DRY WEIGHTS (g)</u>								
Mean leaf weight	0.026	0.154	0.377	0.024	0.101	0.203	0.518	0.092
Mean stem weight	0.009	0.054	0.140	0.007	0.035	0.068	0.169	0.037
Mean root weight	0.004	0.039	0.110	0.003	0.019	0.056	0.150	0.034
Mean total plant weight	0.040	0.247	0.627	0.034	0.156	0.326	0.837	0.159
<u>RATIOS (FINAL)</u>								
Mean Root/shoot ratio (g/g)	0.121	0.189	0.212	0.108	0.145	0.201	0.210	0.043
Mean Stem weight ratio (g/g)	0.233	0.220	0.223	0.202	0.222	0.206	0.198	0.026
Mean height/stem weight (cm/g)	639	262	126	848	370	237	106	97
Mean height/total plant weight (cm/g)	148.4	57.5	28.0	164.1	81.4	47.9	20.5	13.2

Shows raw and derived data for *Terminalia ivorensis* at 5th week. Analysis of variance showed that the differences within treatments were highly significant ( $P < 0.001$ ).



The most striking effect of light quality (low R/FR) on *Terminalia ivorensis* was to increase LAR (Fig. 6.5a) by about ten fold (Table 6.4) whereas *Khaya senegalensis* (Fig. 6.5b) did not show such drastic increases.

From Table 6.3, the following observations were made between treatments for *Terminalia ivorensis*:

- 1) Leaf growth: Under low R/FR there were fewer leaves with a higher leaf area than under high R/FR where there were slightly more leaves with a low leaf area. Also under low R/FR, mean leaf dry weight was higher than under high R/FR with a corresponding PAR.
- 2) Growth in general: Plants grown under low R/FR showed a higher increase in dry weight than those under high R/FR, resulting in higher total plant weight at corresponding PAR.
- 3) Root/Shoot ratio was also higher under low R/FR than under high R/FR with a corresponding PAR.
- 4) Extension growth: Under low R/FR, number of internodes, internode length and stem height were slightly higher than under high R/FR with a corresponding PAR.
- 5) Mean height/Stem dry weight (specific stem length) and mean height/total plant weight decreased with increasing PAR irrespective of R/FR, but were higher under high R/FR than low R/FR with a corresponding PAR.



TABLE 6.4

PAR ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ )	18	125	250	18	125	250	610	LSD at 95 %
RED/FAR RED (R/FR) RATIO	0.14	0.28	0.59	1.64	1.70	1.66	1.77	
Mean number of leaves	3.1	5.1	7.6	2.6	6.0	6.4	7.1	1.0
Mean number of Internodes	1.3	4.0	6.0	0.8	4.5	5.2	6.1	0.88
Mean Internode length (mm)	9.0	18.4	15.7	3.8	17.0	16.4	13.5	4.1
Mean stem height (cm)	8.3	15.0	17.6	9.4	14.3	17.3	15.6	2.9
Mean leaf area ( $\text{cm}^2$ )	5.3	14.7	28.3	5.8	28.8	51.4	77.6	15.1
<u>DRY WEIGHTS (g)</u>								
Mean leaf weight	0.06	0.161	0.307	0.049	0.210	0.419	0.634	0.10
Mean stem weight	0.03	0.071	0.116	0.028	0.083	0.176	0.266	0.05
Mean root weight	0.023	0.048	0.085	0.021	0.070	0.153	0.288	0.05
Mean total plant weight	0.114	0.280	0.508	0.098	0.363	0.748	1.188	0.18
<u>FINAL RATIOS</u>								
Mean Root/shoot ratio ( $\text{g g}^{-1}$ )	0.265	0.209	0.206	0.279	0.237	0.253	0.325	0.06
Mean height/stem weight ( $\text{cm g}^{-1}$ )	286.3	218.8	154.2	344.2	177.8	109.9	67.3	37.7
Mean height/total plant weight ( $\text{cm g}^{-1}$ )	77.0	56.2	34.8	96.5	40.6	25.2	14.4	12.04
Mean stem weight ratio ( $\text{g g}^{-1}$ )	0.264	0.256	0.226	0.282	0.229	0.233	0.219	0.03

Shows raw and derived data for *Khaya senegalensis* at 5th week, analysis of variance showed significant differences within treatments ( $P < 0.001$ ) except in leaf weight ratio ( $P < 0.01$ ).

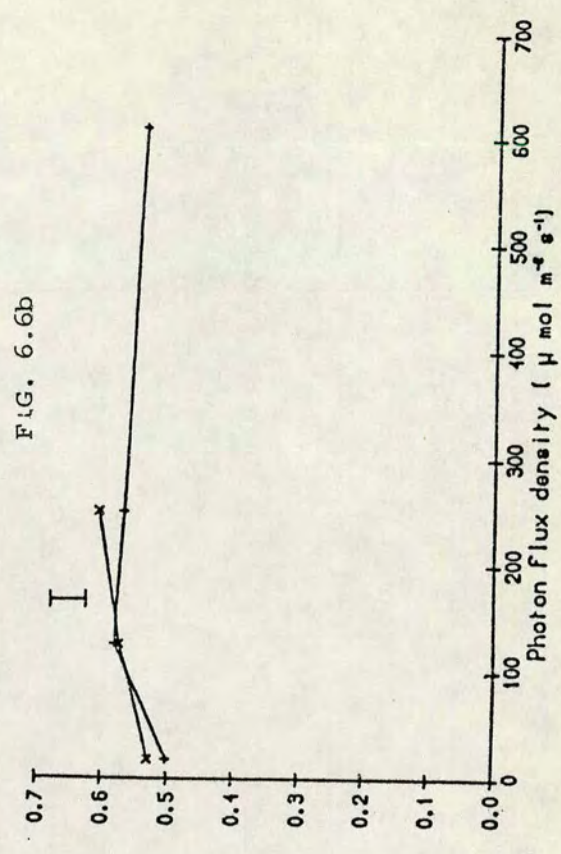
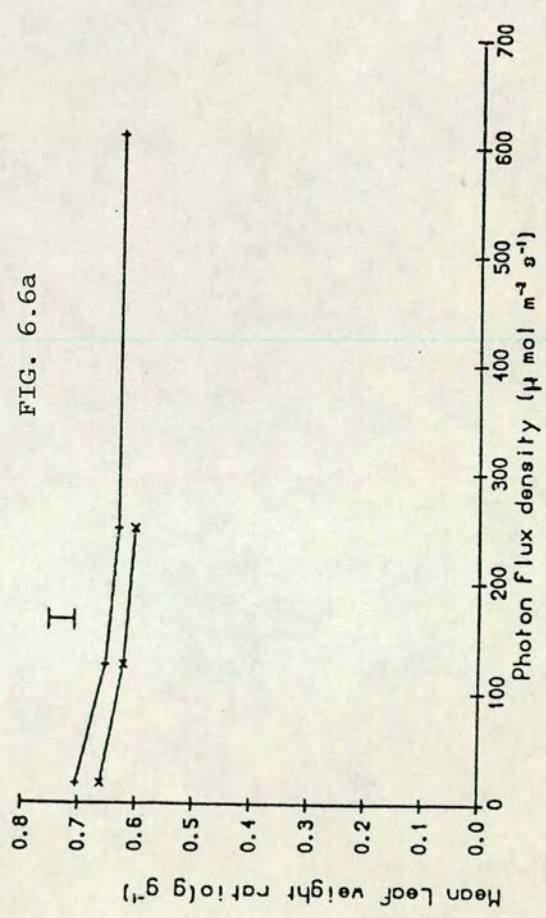
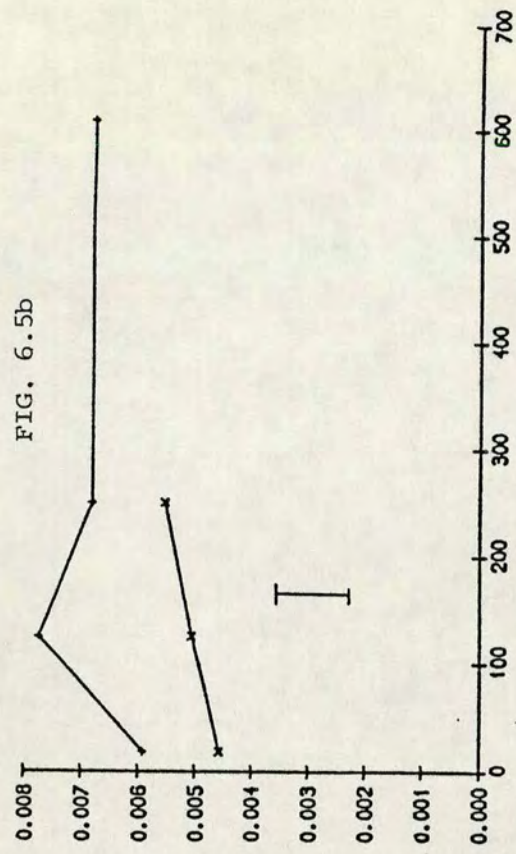
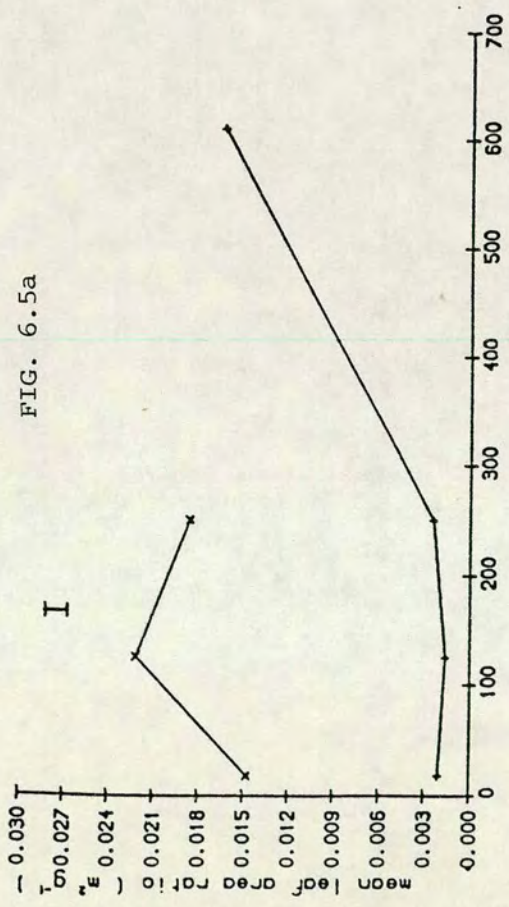


From Table 6.4, the following observations were made between treatments of corresponding PAR.

- 1) The differences between low and high R/FR in leaf production, number of internodes and internode length were less clear-cut than those observed in *Terminalia ivorensis* (Table 6.3). However, under very low PAR ( $18 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) the observed values were higher under low than at high R/FR. Maximum number of internodes were observed at  $250 \mu\text{mol m}^{-2} \text{s}^{-1}$  whereas mean internode length was maximal at  $250 \mu\text{mol m}^{-2} \text{s}^{-1}$  under low R/FR compared to those under high R/FR.
- 2) Leaf growth: Unlike in *Terminalia ivorensis* (Table 6.3) under low R/FR, leaf area was lower than under high R/FR.
- 3) Growth in general: Except under very low PAR, total plant dry weight and root/shoot ratio were higher under high R/FR than under low R/FR.
- 4) Extension growth: Under low R/FR, stem height was higher than under high R/FR.
- 5) Mean height/stem weight (specific stem length) and mean height/total plant weight declined with increasing PAR as observed in *Terminalia ivorensis* (Table 6.3). However, at low PAR ( $18 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), the mean values were higher under low R/FR than those under high R/FR.

Leaf area ratio (LAR) is the product of leaf weight ratio (LWR) and specific leaf area (SLA). Of the two, SLA and LWR, the former is in general more sensitive to environmental changes and more prone to ontogenetic drift. It is also known that shade (reduced photon flux density) causes striking increase in SLA, partly offsetting decreases in NAR (e.g. Hughes and Evans 1962). In both species, leaf weight ratio was almost constant around 0.6 (Fig. 6.6a and 6.6b). Consequently, the most significant changes were in SLA (Figs. 6.7a and 6.7b) especially in *Terminalia ivorensis* where the differences in SLA between leaves developed under low R/FR and high R/FR were also about ten fold





FIGURES 6.5 and 6.6 : The effect of low (x) and high (+) R/FR ratio on the final leaf area ratio (Fig. 6.5) and leaf weight ratio (Fig. 6.6) in *Terminalia ivorensis* (a) and *Khaya senegalensis* (b).



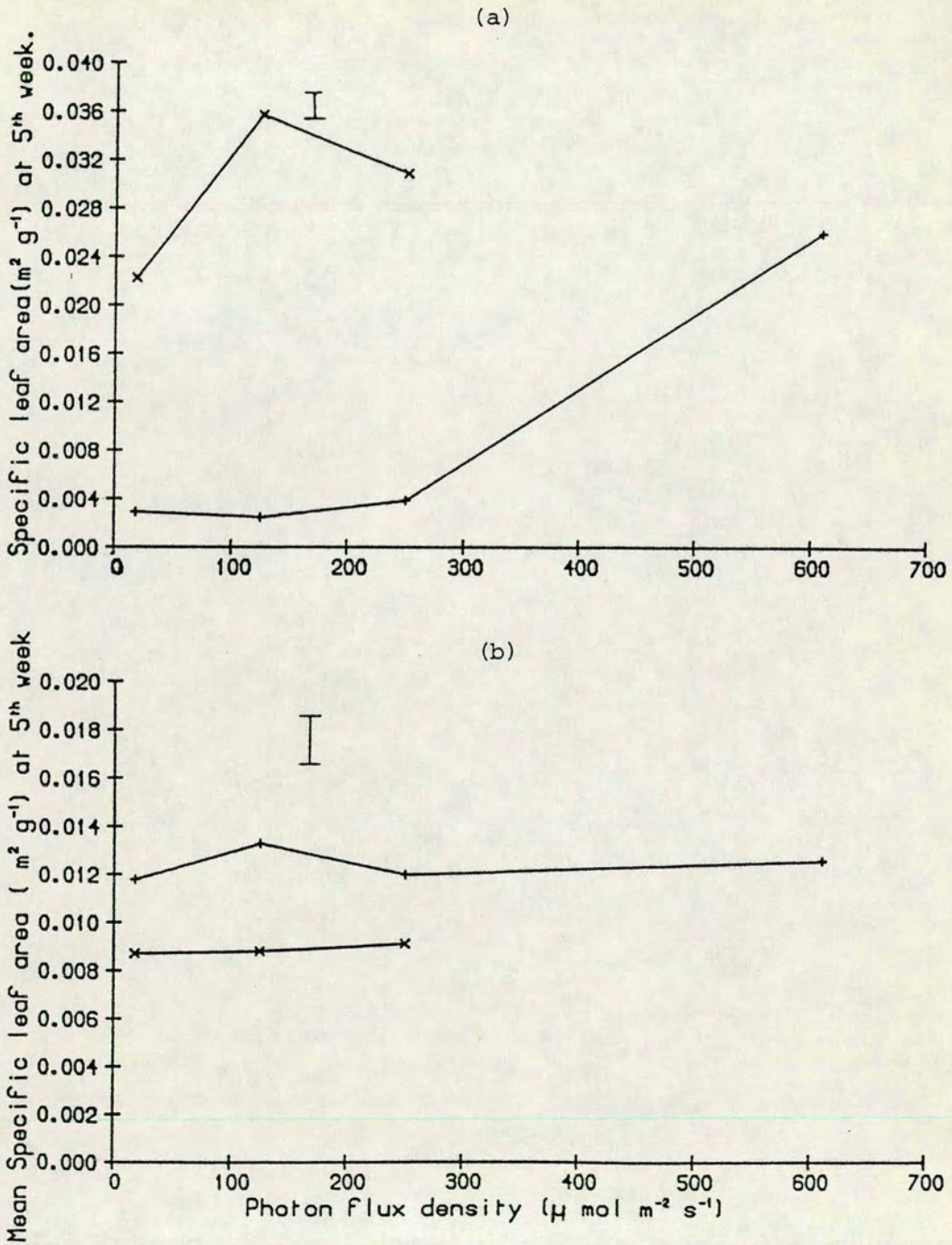


FIGURE 6.7: The effect of low (x) and high (+) R/FR ratio on final specific leaf area in *Terminalia ivorensis* (a) and *Khaya senegalensis* (b).



corresponding to changes in LAR (Figs. 6.5a and 6.7a). This means that in *Terminalia ivorensis*, the leaves developed under low R/FR were thinner whilst those developed under high R/FR were thicker. Again this was not observed in *Khaya senegalensis* (Figs. 6.5b and 6.7b).

### 6.3.3 Stem height/weight ratio (specific stem length)

In addition to calculating the usual parameters of growth analysis, it is instructive to examine other relationships particularly height/weight ratio. Height/weight ratio is usually referred to as specific stem length (SSL) i.e. the length per unit weight. Specific stem length was higher in *Terminalia ivorensis* (Fig. 6.8a) than *Khaya senegalensis* (Fig. 6.8b) and in both species SSL decreased with increasing PAR irrespective of R/FR. It was higher under high R/FR than under low R/FR in *Terminalia ivorensis* (Fig. 6.8a) whilst in *Khaya senegalensis* (Fig. 6.8b) the differences were less clear-cut.

## 6.4 Discussion

The main effect of a reduction in R/FR ratio is to increase specific leaf area in *Terminalia ivorensis*. Other workers, for instance Frankland and Lutendre (1978) found that the leaves of tobacco plants receiving five minutes of R/FR at the end of each eight hour day photoperiod were narrower and thinner than those receiving red light throughout, though specific leaf area remained unchanged. Smith (1983) in specially constructed growth cabinets found that specific leaf area was higher at R/FR ratio ( $>2.0$ ) in *Chenopodium album*, a shade avoider. In the earlier literature, it is suggested that with respect to leaf development, reduced photon flux density of shade conditions might be more important than changes in R/FR ratio. However, under natural conditions, changes in light quantity never occur without simultaneous changes in light quality (Smith 1983). Plants growing in natural shade adapt to make maximum use of available light through increased leaf area and specific leaf area (e.g. Corré 1983).



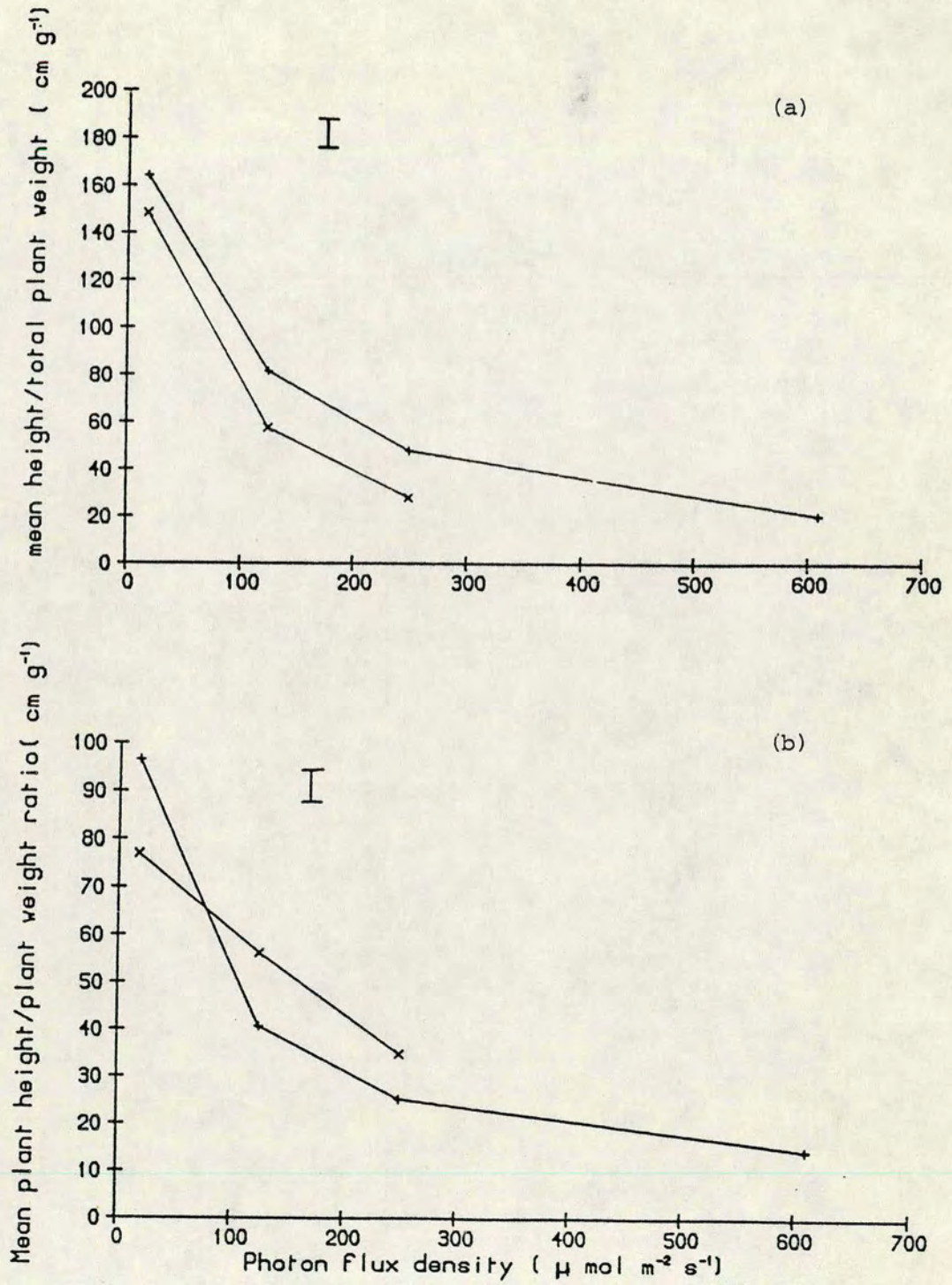


FIGURE 6.8: The effect of low (x) and high (+) R/FR ratio on final plant height/weight ratio in *Terminalia ivorensis* (a) and *Khaya senegalensis* (b).



Corré (1983) found that under a low R/FR ratio, leaves were thinner and this did not seem to depend on shade tolerance in the species he investigated. At the same time, the influence of photon flux density on specific leaf area was clear: leaves of most species were much thinner in low photon flux density. He also found that leaf area ratio decreased greatly in sun species but only weakly in shade species. He concluded that leaf thickness showed no clear difference between sun and shade species, since the leaf thickness primarily depends on the amount of energy that is fixed in leaves, and therefore could depend much more on the intensity than on the quality of light.

In other experiments the effects of R/FR on leaf thickness seem to be less clear (see Section 3.3.2.3). In aquatic species of *Potamogeton* the differences in specific leaf area were attributed to differences in daily light levels than to any changes in light quality; although R/FR ratio might be extremely important in determining leaf shape in some other aquatic plants (e.g. Spence 1981).

It is clear from the above that SLA has not been associated with low R/FR specifically, but to an overall reduced photon flux density. The increase in SLA at low R/FR in *Terminalia ivorensis* can be considered as one of the responses to competition with other species in the gap, by developing thin leaves with more area. This perception mechanism has ecological consequences: *Khaya senegalensis* did not show such drastic increase in SLA, possibly it was insensitive to R/FR at the stage of development, whilst *Terminalia ivorensis* behaved as the aggressive ruderals described by Smith (1981). High SLA increased LAR more than it decreased NAR and so the result was a higher RGR in *Terminalia ivorensis* than *Khaya senegalensis*. Under the un natural high R/FR in the experiment, *Terminalia ivorensis* responded to the PAR levels by producing more leaves with a very low leaf area with a consequent low SLA and LAR, resulting in increased NAR with a decreased RGR whilst *Khaya senegalensis* responded by slight increase in RGR.



#### 6.4.1 Other aspects of growth analysis: NAR and RGR

It is not possible to make a detailed comparison of the performance of different species using information available in the literature as the environmental conditions have not usually been fully specified (e.g. Synnott 1975), besides there are no cases where RGR and NAR of tropical tree seedlings have been investigated both as a function of R/FR and PAR. However, in herbaceous sun and shade plants, Corré (1983) showed that reduced photon flux density markedly reduced NAR and RGR. Under a low R/FR ratio, the RGR decreased in all species, because of a lower NAR; in the sun species the decrease occurred because of a lower leaf area ratio. The decrease in RGR was much greater in sun species, some of which even stopped growing, whereas all shade-tolerant species continued to grow healthily, albeit slowly. These results can only be compared to those reported for the previous experiment (Chapter 5).

The values for NAR in this experiment were much higher under high R/FR in *Terminalia ivorensis* (Fig. 6.4a), and for both low and high R/FR ratios in *Khaya senegalensis* (Fig. 6.4ab) than those reported in the literature for reduced photon flux density (e.g. Jarvis and Jarvis 1964) and for tropical trees (e.g. Okali 1971, 1972; Fasehun and Audu 1980). Therefore comparisons based on Tables 6.5 and 6.6 of RGR and NAR must be treated with caution. Light regimes were usually characterized in terms of % full sunlight, not in absolute units of energy, and temperature and humidities differed greatly. Besides, the age of the seedlings was also variable. It is not surprising therefore, that the results of NAR in this experiment are sometimes different from other estimates by a factor of ten. However, the data in the literature serves a useful purpose for comparisons. In addition, there is need for more elaborate work especially on tropical tree species.

#### 6.4.2 Specific stem length (SSL)

*Terminalia ivorensis* showed a higher specific stem length (Fig. 6.8a) about twice that of *Khaya senegalensis* (Fig. 6.8b) at very low



TABLE 6.5

SPECIES	LIGHT REGIME (Approximate % of full day light)					
	1 - 4	5 - 7	10	18 - 25	40 - 55	100
<i>Entandrophragma utile</i>	0.028		0.07			0.095
<i>Trema guineensis</i>					0.37-0.82	
<i>Musanga cecropioides</i>					0.14	0.18
<i>Helianthus annuus</i>			0.10		0.77-1.1	0.54-1.5
<i>Theobroma cacao</i>				0.07-0.09		
<i>Nauclea diderrichii</i>	0	0.045		0.049		0.047
<i>Aukomea klatineana</i>	0.004	0.032		0.037		
<i>Khaya grandifoliola</i>	0.007	0.024		0.025		
<i>Khaya ivorensis</i>					0.18-0.31	
<i>Khaya senegalensis</i>					0.15-0.18	
<i>Ceiba pentandra</i>		0.02	0.10		0.27	0.3-0.56
<i>Terminalia ivorensis</i>	0	0.10			0.6	0.31-0.68
<i>Chlorophora excelsa</i>		0.10	0.09		0.25	0.24-0.28
<i>Pericopsis excelsa</i>		0.05		0.13		0.17
<i>Alouasia macrorrhiza</i>	0.018					
<i>Khaya senegalensis</i> (1)		0.002		0.01	0.08	0.155
<i>Khaya senegalensis</i> (2)	0.09	0.27	0.39		0.55	
<i>Terminalia ivorensis</i> (1)		-0.062		-0.06	0.016	0.212
<i>Terminalia ivorensis</i> (2)	0.066	0.43	0.62		0.66	

Shows comparisons of RGR ( $\text{g g}^{-1} \text{ week}^{-1}$ ) for tropical tree species and *Helianthus annuus* (adapted from Synnott, 1975); (1) data for the preliminary glasshouse experiment (Chapter 5) and (2) data for this experiment for low R/FR and values for high R/FR at  $610 \mu\text{mol m}^{-2} \text{s}^{-1}$ . The assumption of conversion was that full day light  $\approx 2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ . There is little evidence that R/FR ratio has been used to characterise RGR.



TABLE 6.6

SPECIES	LIGHT REGIME (Approximate % of full daylight)							
	1 - 4	5 - 7	10	18 - 25	40 - 55	100		
<i>Entandrophragma utile</i>	1,1		4			11		
<i>Trema guineensis</i>					15 - 31			
<i>Musanga cecropioides</i>					6 - 10	20		
<i>Helianthus annuus</i>			3		34 - 43	63 - 70		
<i>Theobroma cacao</i>				7 - 9		20		
<i>Nauclea diderrichii</i>	0	15		20		23		
<i>Aukomea klaineana</i>	1,0	9		13				
<i>Khaya grandifoliola</i>	3,5	11		13				
<i>Khaya ivorensis</i>					23 - 29			
<i>Khaya senegalensis</i>					11			
<i>Ceiba pentandra</i>		3	5		28	54 - 60		
<i>Terminalia ivorensis</i>		0	2		22	40 - 60		
<i>Chlorophora excelsa</i>		1,0	.2		10	14		
<i>Pericopsis elata</i>		2,2		7		16		
<i>Khaya senegalensis</i> (1)		0,5		0,9	7,3	17,8		
<i>Khaya senegalensis</i> (2)	17,8	50,3	70,0		90,6			
<i>Terminalia ivorensis</i> (1)		-7,7		-5,8	1,7	24,7		
<i>Terminalia ivorensis</i> (2)	4,5	22,5	35,9		42,7			

Shows comparisons of NAR ( $\text{g m}^{-2} \text{ week}^{-1}$ ) for tropical tree species and *Helianthus annuus* (adapted from Synnott, 1975); (1) data for the preliminary glasshouse experiment (Chapter 5) and (2) is data for this experiment for low R/FR values and high R/FR (at  $610 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ). It was assumed that full daylight was  $\approx 2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ .



photon flux densities with or without a variation in R/FR. Specific stem length responded to overall reduced photon flux density in (the light demander) *Terminalia ivorensis*, as it was higher at high R/FR than low R/FR. This is in agreement with Morgan and Smith (1977) who pointed out that stem extension response to simulated shade has a systematic relationship to species habitat; that species from the open habitats react by large increases in stem extension rate whilst species from woodland or shade habitats react less strongly or not at all. Morgan and Smith (1981) stressed that these two classes of response may have ecological significance; for instance, species from open habitats may over-top herbaceous vegetation canopy. According to Smith (1981; 1982), sun species avoid shade by mobilizing all available carbohydrates and by greatly increasing stem extension at the expense of development of leaf area whilst shade species show a conservative use of assimilates, resulting in slow-growth, and only a slight reaction to the light quality component of shade.

The results of this experiment on SSL are also in agreement with Corré (1983) and Smith (1983) who reported that *Chenopodium album*, *Urtica dioica* and *Teucreum scorodina* seedlings that represent the open, hedgerow and woodland habitats; showed marked increases in SSL under low PAR values. This meant that those species produced the same length of stem with less material. Smith (1983) also showed that these species achieved their high SSL by responding to R/FR.

This and other results point to the fact that R/FR rather than PAR is sensed by the plants to assess and respond to the degree of shading by other vegetation. The R/FR ratio is indeed much more critical; it varies much less with weather conditions and also time of the day, so a rapid functional response is possible (Smith, 1982) as experienced in the gap sunflecks (Pearcy, 1983).

These two species reacted systematically differently to the R/FR ratios. At low R/FR, *Terminalia ivorensis* showed more elongation, a higher specific stem length and a correspondingly higher leaf area ratio as a result of a higher specific leaf area than *Khaya senegalensis*. Because of these morphogenetic adaptations, the light demander showed



an appreciable increase in RGR. At high R/FR ratio, *Terminalia ivorensis* produced thick leaves with a very low leaf area that resulted in an increased overall carbon assimilation rate with a low RGR.

The general differences between species in their response to shade are those related to ecological distribution. One way of interpreting these results is to imagine a situation at the forest floor of a closed forest canopy (Section 2.4): survivors are those that do not grow tall, but remain short and maintain a positive carbon balance (e.g. Section 5.2.2.1, Figs. 5.6b and 5.7b). It is most likely that under these conditions, light demanders may be present as seeds in the seed bank of the forest floor. When a big tree falls to make a relatively small gap, shade tolerant species such as *Khaya senegalensis* may be at an advantage through a high initial relative growth rate. However, in this experiment *Khaya senegalensis* did just as well as *Terminalia ivorensis* when the R/FR was high. The ability to detect changes in R/FR would place *T. ivorensis* at an advantage: when the R/FR was low, RGR was enhanced. Nevertheless, *Khaya senegalensis* displayed twice as much overall carbon assimilation as *Terminalia ivorensis* at all levels of corresponding PAR. Such responses as observed in *Khaya senegalensis* would enable the shade tolerant species to maximize their photosynthetic efficiency in say the sunflecks associated with such gaps (e.g. Björkman and Ludlow 1972; Pearcy 1983). Morphogenetic responses as a result of changes in R/FR as observed in *Terminalia ivorensis* would enable the light demander to grow out of shade.

On the other hand, if we imagine a situation in a large gap (Section 2.2) say after a natural disturbance, strong interspecific competition involving tree seedlings and herbaceous plants is more likely. Survivors are the ones that can detect vegetational shade (Section 2.5) and respond by growing tall and fast. *Terminalia ivorensis* does this by:

- a) increasing specific stem length in response to reduce PAR and
- b) increasing relative growth rate in response to reduced R/FR.

The latter is achieved mainly via the R/FR-induced increase in specific



leaf area. *Khaya senegalensis* does not possess these characteristics: although the specific stem length is increased to some extent, its RGR is somewhat reduced by the reduction in R/FR. The inability to detect the changes in R/FR ratio means that *Khaya senegalensis* would be shaded by species like *Terminalia ivorensis*.



## CHAPTER SEVEN

**THE EFFECT OF HIGH AND LOW PHOTON FLUX DENSITY ON SPECIFIC  
LEAF AREA AND CHLOROPHYLL CONTENT IN SOME TROPICAL TREE  
SEEDLINGS AND THE GIANT SEDGE**

## 7.1 Introduction

Chlorophyll content in plant tissues is often determined as a routine analysis in ecological and physiological investigations (Linder, 1974). In the IPB handbooks No. 2 (Newbould, 1967) and No. 6 (Milner and Hughes, 1968) it is recommended that the amount of chlorophylls should be used as one measure of the size of the photosynthetic system. The leading role of the chlorophylls in absorption of radiant energy and their participation in photosystems, transforming the absorbed radiant energy into chemical energy has been known for many years. This is the main reason why photosynthetic activity is sometimes expressed per amount of total chlorophyll content (a + b) or chlorophyll a only (Šesták et al., 1971).

However, chlorophyll content of photosynthetic organs varies according to plant species (genetic potential), leaf position, age and growth phase, grade of ecotypic adaptation and environmental conditions particularly irradiance, temperature, water stress and nutrition (e.g. Morales et al., 1982); and chlorophyll formation is very sensitive to almost any factor which disturbs metabolic processes. The capacity of leaves to photosynthesize varies with the season and the environment in which the leaves have developed (Bourdeau and Laverick 1958; Bourdeau 1959; Senser et al., 1975; Lewandowska and Jarvis 1977) in particular, the light environment during leaf growth and development has been shown to have large effects (Björkman and Holmgren 1963; Björkman et al., 1972). Relatively low photon flux densities are effective in initiating or promoting chlorophyll formation whilst very high photon flux density causes a net decomposition of chlorophyll, with the decomposition rate exceeding the rate of synthesis.

One of the most studied environmental factors affecting



chlorophyll content per area of leaf is that of irradiance during leaf development. It is in this respect that leaves can be differentiated into 'sun' and 'shade' leaves. For instance, it is known that shade leaves usually have a higher concentration of chlorophyll than sun leaves. There also is a higher proportion of chlorophyll a to b in sun than in shade leaves. Chlorophyll content is also known to depend on the ecological status of the species: Björkman and Holmgren (1963) showed much variation between species found consistently in 'shaded' habitats as opposed to those occurring in the 'open'. Such studies have been mainly done on temperate tree species and herbaceous plants. Unfortunately, there is almost no published data on tropical tree species linking light regime to photosynthetic rates and chlorophyll content.

Within a tropical moist forest, it is generally assumed that variation in the physical environment, especially air and soil temperature, soil moisture and photon flux density in the gaps (Chapter 2, section 2.3) is higher than in the closed canopy habitats (e.g. Bazzaz, 1979). The variability in the energy environment is related mainly to the amount of energy received at the top of the canopy, its attenuation by vegetation and the way in which it is dispersed (Bazzaz and Carlson, 1982). The frequency of occurrence of environmental extremes is thought to be higher in large gaps compared with that of the closed canopy habitats due to the reduced environmental buffering associated with such large gaps. These and other differences uncovered between habitats are thought to have selected species with specific adaptations to each environmental regime. For example, higher rates of photosynthesis, transpiration and respiration, stomatal and mesophyll conductances; have been repeatedly measured for light demanders as compared to shade tolerators (e.g. Loach 1967; Larcher 1969; Boardman 1977; Bazzaz 1979). The level of photon flux density required for photosynthetic saturation is lower for shade tolerant species (e.g. Grime 1977, Bazzaz and Pickett 1980; see Chapter 9 of this thesis). Plants of open habitats may also respond plastically and acclimate rather quickly to changes in environmental conditions such as temperature. The degree of flexibility of different species to acclimate to environmental extremes must itself be related to the level



of environmental variation that is characteristic of the habitat in which the species is normally found. For example, Pearcy (1983) observed a ten-fold difference in the number and duration of sunflecks between sample sites in a Hawaiian forest understorey and found that growth of saplings was highly correlated with the estimates of the duration of sunflecks; as did Björkman and Ludlow (1972) in Australian sub-tropical forests. Björkman and Powles (1981) found that in large gaps, sunflecks reaching the forest floor produced a drastic change in photon flux density of up to 200-fold. Such increase in photon flux density is believed to have deleterious effects on the photosynthetic systems of the plant by photo-oxidation (Briggs, 1981).

Laboratory studies have shown that transfer of shade plants to high photon flux densities induces conspicuous changes in chloroplast morphology, and chlorophyll is destroyed by photo-oxidation (e.g. Gauhl 1969, 1970) and heat (Sato 1970; Ageeva 1977). The loss of photosynthetic efficiency is due to the destruction of reaction centres. Photosystem II (PS2) is more sensitive to such damage (Björkman 1968b). Nevertheless, accessory pigments such as carotenoids are believed to offer protection in such circumstances.

The aim of this chapter is to investigate variations in leaf properties such as chlorophyll content, chlorophyll a/b ratio and specific leaf area in several tropical tree species and a giant sedge *Cyperus papyrus*. In the previous chapter (Chapter 6) it was shown that whereas morphogenesis responded to R/FR, net assimilation rate responded to photon flux density of the PAR. In this experiment, R/FR was not measured. Shade under low photon flux density was achieved by two layers of muslin material beneath the seedling and soil trays. It is possible that initially the R/FR ratio did not differ in the two light regimes.

The species were grown under standard conditions in a Fisons growth cabinet at high photon flux density (HPD)  $\approx 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  and at low photon flux density (LPD)  $\approx 40 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; in order to investigate the influence of photon flux density on photosynthetic systems.



After three weeks of growth at the above light conditions, a transfer of replicates was made in both directions to assess the damage on the photosynthetic apparatus due to photo-oxidation. Thus a leaf which had developed under LPD was transferred to HPD and other leaves from HPD to LPD. Comparisons of chlorophyll content, chlorophyll a/b ratio and specific leaf area of leaves which had undergone a recent step-wise change in light regime were made with replicates which remained in the initial growing conditions. The extent of chlorophyll degradation and chlorophyll synthesis were noted.

Chlorophyll content (a, b and a + b) was determined on both unit leaf area and leaf dry weight basis. Leaf area is probably the most relevant basis on which to express chlorophyll content (Linder, 1974) as it is closely related to the light intercepting function of the leaf. Leaf dry weight, as a basis, clearly is sensitive to metabolic changes that take place in the leaf under certain environmental conditions such as variations in photon flux density. Chlorophyll content was not expressed on fresh weight basis because this changes with water content of the tissue (Šesták *et al.*, 1971).

At the end of the experiment, the photosynthetic characteristics of the leaves developed under LPD and HPD were investigated. In this chapter the results of chlorophyll determinations are reported and discussed. In chapter nine, the photosynthetic measurements ( $\text{CO}_2$  assimilation rates) will be described and an attempt made to discuss the relationship between the chlorophyll content recorded and photosynthetic characteristics observed.

## 7.2 Materials and methods

### 7.2.1 Plant material

Initially the widest possible range of light demanders and shade tolerators were to be raised from seed in two light regimes : high photon flux density (HPD)  $\approx 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  and low photon flux density (LPD)  $\approx 40 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Ecological characteristics of the species, number of seeds, source of seeds, batch numbers and dates of



collection are presented in Table 7.1 below:

Ecological Characteristics	Species	Number of Seeds	Seed source, FRIN batch number and dates of collection
Light demanding trees and C <sub>3</sub> photosynthesis	<i>Terminalia</i>	100	Okuri-Ikomo (Nigeria)
	<i>ivorensis</i>		6688, 9/12/81
	<i>Terminalia</i>	100	Bakatari (Nigeria)
	<i>superba</i>		4078, 11/1/77
	<i>Triplochiton</i>	100	9 km to Okura-Lafia
	<i>scleroxylon</i>		Rest house Ayangba/ Ankpo Road (Nigeria) 16/3/80
	<i>Chlorophora</i>	100	Idi Ishin, Ibadan
	<i>excelsa</i>		(Nigeria) 5552: 1982
	<i>Maesopsis eminii</i>	60	Makerere University campus (Uganda) July 1982
	<i>Nauclea</i>	many	HQRS (New Quarters)
	<i>diderrichii</i>	tiny seeds	Nigeria, 5422 : 5/12/77
Shade tolerating trees and C <sub>3</sub> Photosynthesis	<i>Khaya senegalensis</i>	100	Tabeta Mokwa (Nigeria) 5966 : 29/1/80
	<i>Khaya ivorensis</i>	100	Agunrege Saki Road (Nigeria) 6719 : 2/2/82
	<i>Entandrophragma</i>	100	Kho-137 Ohuku Road
	<i>angolensis</i>		(Nigeria) 6470 : 5/12/80
Sedge, light demanding, and C <sub>4</sub> photosynthesis	<i>Cyperus</i>	many	Botanic Gardens
	<i>papyrus</i>	tiny seeds	(Dundee) from Lake Chad.

\*FRIN = Forestry Research Institute of Nigeria.



The seeds of each species were divided into four equal portions and sown in seed trays in UC 50:50 soil mixture. They were transferred to the Fisons growth cabinet (Fisons Environmental cabinet type 2340, Fisons Scientific Apparatus, Loughborough, U.K.) on 23/2/83.

As a precaution, a set of seeds was also sown under the glasshouse mist bench conditions (only two species came from a different stock of recent seeds): *Terminalia superba* from tree 1 at Omnigambari, Nigeria; collected on 30/8/82 and *Khaya senegalensis* (6719) from Agunrege Shaki Road, Nigeria; collected on 2/2/82. They were sown on 9/3/83. After two days on the mist bench, the trays were covered with a white polythene sheet to maintain warmth and moisture.

### 7.2.2 Growth cabinet and conditons of the experiment

The experiment was conducted in the Fisons growth cabinet. Important features of this growth cabinet (Fig. 7.1) are :

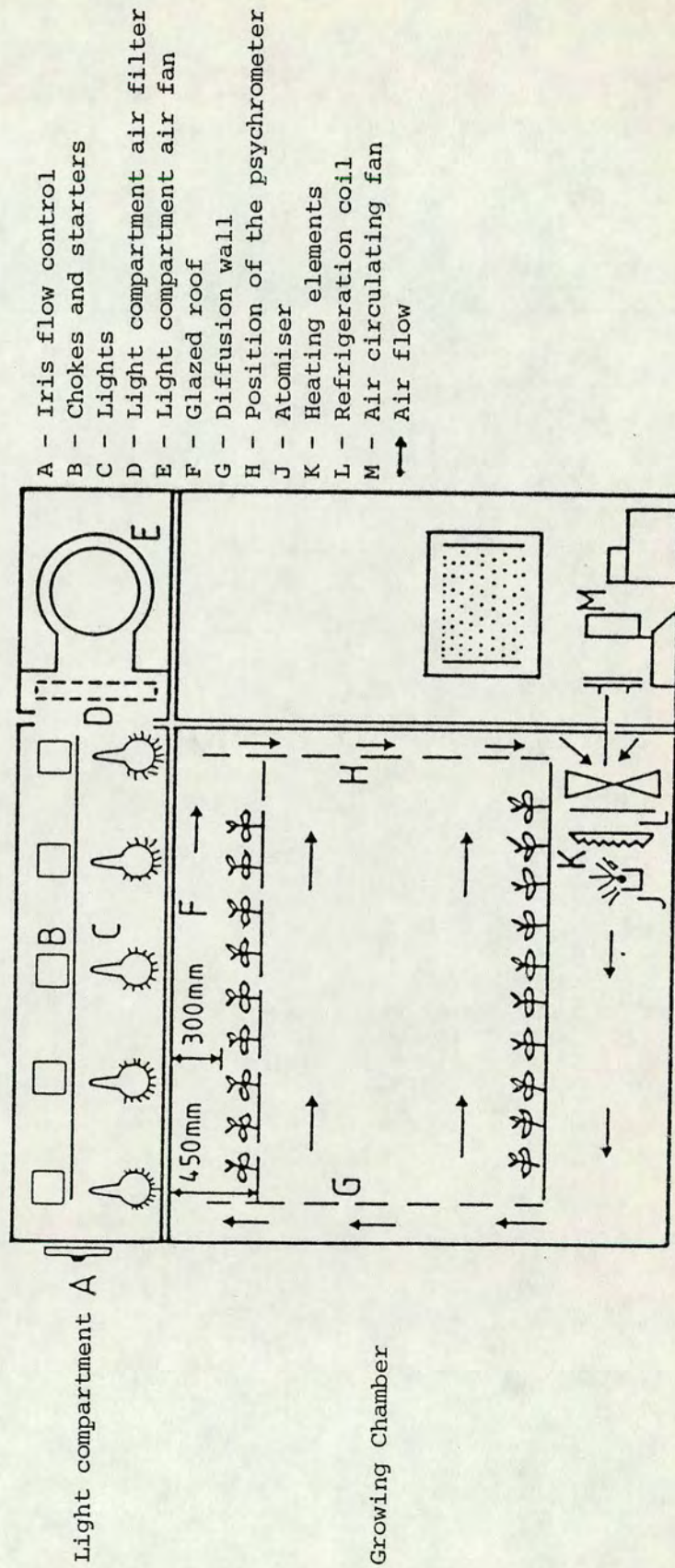
(a) Light: Over the growing chamber a double-glazed roof separates the chamber from the light compartment above. The light compartment houses 21 high intensity metal halide lamps (Wotan, Type HQ1-2, 250 W/NDL) plus 12 pearl bayonet tungsten 100 W lamps. At 300 mm from the light compartment, a combination of these lamps produced a flux density of about  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  or  $3000 \mu\text{mol m}^{-2} \text{s}^{-1}$  at zero distance. These lamps were chosen to simulate daylight as far as possible. The two levels of photon flux density were achieved as illustrated in Fig.7.1. Spaces between seed trays allowed light to pass to the lower plants, being transmitted also through two layers of muslin supported beneath the top trays.

(b) Temperature: Air temperature could be controlled to an accuracy of  $0.5^{\circ}\text{C}$  in the range of  $0-50^{\circ}\text{C}$ . Mercury in-glass thermometers inserted in dry soil and seed trays at about  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  showed that the seed trays had a soil temperature of between  $30-32^{\circ}\text{C}$  depending on their state of wetness. In the seed and soil trays at  $\approx 40 \mu\text{mol m}^{-2} \text{s}^{-1}$ , the soil temperature was  $28-29^{\circ}\text{C}$ . Air temperature in the cabinet was  $30 \pm 0.5^{\circ}\text{C}$  and differed much less than did soil temperature.



FIGURE 7.1: Important features of the Fison s Growth Cabinet:

# The Fisons growth cabinet.



The plants at the top received  $\approx 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  (HPD) whilst those at the bottom received  $\approx 40 \mu\text{mol m}^{-2} \text{s}^{-1}$  (LPD) (Serial No. 4844, type 2340, G3 Horizontal).



(c) Air flow: Flow was horizontal and laminar with velocities of  $1 \text{ m s}^{-1}$  in the upper chamber, and reduced to  $0.6 \text{ m s}^{-1}$  in the lower chamber. Air velocities were high enough to ensure that no appreciable local microclimate developed in the growing chamber but not so high as to unduly disturb the plants. Temperature and humidity were sensed with a movable psychrometer which fed back signals to the controllers and indicators.

(d) Humidity: To increase humidity, finely atomized water is automatically sprayed onto the heating elements causing the water to vapourise. Humidity is reduced by condensation on surfaces at or below the dew point. To sense humidity, air flowed over wet and dry resistance thermometers (RT) located within the psychrometer. The wet RT's were kept permanently wet by wicks fed from distilled water reservoirs. The RT's were connected to an electronic controller which fed back signals denoting the temperature differential. The signal was compared with the desired value (set point) and errors corrected by actuating an atomizer on a time proportioning basis, and adjusting the surface temperature of an evaporator coil (refer to the Fisons Instrument, Handbook No. K94, section 2.2.2).

(e) Conditions set for this experiment:

Photoperiod	= 12 hours
Day temperature	= $30 \pm 0.5^{\circ}\text{C}$
Night temperature	= $25 \pm 0.5^{\circ}\text{C}$
Relative humidity	= $85 \pm 1\%$
SVPD at $30^{\circ}\text{C}$	= 6.2 mbar
SVPD at $25^{\circ}\text{C}$	= 4.9 mbar

### 7.2.3 Experimental design

About 320 seedlings would fit in the growth cabinet using a minimum size of pot (11 cm high and 9 cm top-diameter). Half the number were maintained under HPD and the other half under LPD. With 10 species this meant 32 plants per species, 16 plants per treatment; and two replicates of 8 plants in each of the treatments (LPD and



HPD ). Thus, under HPD and LPD 4 replicates of 7 plants were analysed throughout the experimental period as shown in Figs. 7.2a - 7.2d.

As there were minor differences between species in leaf size, production and longevity, there were of necessity, minor differences between the treatments given to different species. Minor experimental comparisons were also incorporated in these schemes to assess the effects of leaf aging and leaf removal, both factors which otherwise would end up inextricably confounded with the light treatments.

All the plant species under both HPD and LPD were randomly distributed and moved around within their light regime once a week. Those under LPD were watered once every two days whilst those under HPD were watered once every day.

### 7.3 Treatment description

The following schemes (Figs. 7.2a - 7.2d) summarize the sequence of events for analysis of leaves for chlorophyll content, chlorophyll a to b ratio and specific leaf area. Each species was considered separately; and in *Triplochiton scleroxylon*, the seedlings which germinated in the growth cabinet were called *Triplochiton scleroxylon* I whereas those which germinated under the glasshouse mist bench conditions and transferred to the growth cabinet were called *Triplochiton scleroxylon* II.

These schemes are necessarily complex as it was felt essential to measure chlorophyll levels at various stages in the development of the plant, and moreover to carry out the transfers from one regime to another both on leaves which had already expanded and those which were in an early stage of expansion.



7.3.1 *Terminalia superba*, Fig.7.2a

		Analysis dates :		
Growth conditions	Seedling replicates	18/4/83	24/4/83	1/5/83
High photon flux density (HPD) $\approx 1000 \mu\text{mol m}^{-2}\text{s}^{-1}$	7	1	→ 3	→ 9
	7	1	→ 4	→ 14
	7	1	→	→ 11
	7	1	→ 8	→ 13
Low photon flux density (LPD) $\approx 40 \mu\text{mol m}^{-2}\text{s}^{-1}$	7	2	→ 6/7	
	7	2	→ 5	
	7	2	→	→ 12
	7	2	→	→ 10

Fig. 7.2a summarises the sequence of events on the plants which were grown under HPD and LPD. 56 plants in replicates of 7 seedlings were transplanted to the growth cabinet on 28/3/83; 28 seedlings under both HPD and LPD. The numbers (1 - 14) represent treatment codes at the time of chlorophyll determination and the arrows represent transfers and time involved (one or two weeks) as described :

- 1 = 3 weeks growth at HPD
- 2 = 3 weeks growth at LPD
- 3 = 4 weeks growth at HPD, third leaf analysed in treatment 1
- 4 = 4 weeks growth at HPD
- 5 = 4 weeks growth at LPD
- 6 = 3 weeks growth at HPD, transferred to LPD for a week; fully expanded
- 7 = same as in 6 except that leaves fully developed after a week in LPD
- 8 = 3 weeks LPD, transfer to HPD for a week, fully developed leaf
- 9 = same plants as in 1 and 3, but different leaf
- 10 = 5 weeks growth LPD (same plants as in 2)
- 11 = 5 weeks HPD



12 = 5 weeks LPD

13 = 3 weeks LPD, 2 weeks HPD (see origin of treatment 8)

14 = 5 weeks HPD (same plants as in 4)

### 7.3.2 *Triplochiton scleroxylon* 1, Fig.7.2b

Growth conditions	Seedling replicates	23/3/83	30/3/83	7/4/83
HPD $\approx 1000 \mu\text{mol m}^{-2}\text{s}^{-1}$	8	2	3	11/12
	7	2	6/7	13
LPD $\approx 40 \mu\text{mol m}^{-2}\text{s}^{-1}$	10	1	4/5	10
	6	1	8	9

Fig. 7.2b shows the sequence of events and treatments: The unequal number of seedling replicates was due to unequal germination under LPD and HPD in the four trays in the growth cabinet. Treatments codes 1 - 13 are :

- 1 = 3 weeks after germination under LPD
- 2 = 3 weeks after germination under HPD
- 3 = 4 weeks under HPD (same plants as in 2)
- 4 = 3 weeks HPD, fully expanded leaves transferred to LPD for one week
- 5 = same plants as in 4, leaf which matured after transfer from LPD to HPD
- 6 = 3 weeks growth under LDP, transferred to HPD, fully expanded leaf after 1 week at HPD
- 7 = same plants as 6, leaf which matured after one week of transfer from LPD to HPD
- 8 = 4 weeks after germination under LPD (same plants as in 1)
- 9 = 5 weeks under LPD (same plants as in 1 and 8)
- 10 = 3 weeks HPD, 2 weeks after transfer to LPD (same plants as 2, 4 and 5)
- 11 = 5 weeks HPD, fully expanded leaf (same plants as in 2 and 3)



- 12 = 5 weeks HPD, young leaf (as in 11)  
 13 = 3 weeks LPD, 2 weeks after transfer to HPD (same plants as 1, 6 and 7).

The above treatments represent the seedling which germinated under the growth cabinet conditions.

### 7.3.3 *Triplochiton scleroxylon* II, Fig.7.2c

Growth conditions	Seedling replicates	18/4/83	25/4/83	1/5/83
HPD $\approx 1000 \mu\text{mol m}^{-2}\text{s}^{-1}$	7	1	→ 3	→ 10
	7	1	→ 4	→ 16
	7	1	→	→ 12
	7	1	→ 8/9	→ 14
LPD $\approx 40 \mu\text{mol m}^{-2}\text{s}^{-1}$	7	2	→ 6/7	→ 15
	7	2	→ 5	
	7	2	→	→ 13
	7	2	→	→ 11

Fig. 7.2c shows the sequence of events on the plants which were grown under both HPD and LPD at the time of chlorophyll content and SLA analysis. The treatments are represented by codes (Numbers 1 - 16) and the arrows show the sequence of transfers after each treatment analysis.

The codes 1 - 16 are :

- 1 = 3 weeks after transfer to HPD  
 2 = 3 weeks after transfer to LPD  
 3 = 4 weeks under HPD (same plants as in 1)  
 4 = 4 weeks under HPD  
 5 = 5 weeks under LPD  
 6 = 3 weeks HPD, fully expanded leaf analysed after transfer to LPD for one week



- 7 = 3 weeks HPD, leaf which matured after growth under LPD for one week
- 8 = 3 weeks LPD, fully expanded leaf analysed after transfer to HPD for a week
- 9 = 3 weeks LPD, leaf which matured after growth under LPD for one week
- 10 = 5 weeks HPD; same plants as in 1 and 3
- 11 = 5 weeks LPD, same plants as 2
- 12 = 5 weeks HPD, same plants as 1
- 13 = 5 weeks LPD, same plants as in 2
- 14 = 3 weeks LPD, two weeks after transfer to HPD; same plants as in 8 and 9
- 15 = 3 weeks HPD, two weeks after transfer to LPD; same plants as in 6 and 7
- 16 = 5 weeks HPD, same plants as in 1 and 4

#### 7.3.4 *Khaya senegalensis*, Fig. 7.2d

Growth conditions	Seedling replicates	18/4/83	25/4/83	1/5/83
HPD $\approx 1000 \mu\text{mol m}^{-2}\text{s}^{-1}$	7	1	→	9
	7	1	→ 3	→ 13
	7	1	→	10
	7	1	↘	7/8
LPD $\approx 40 \mu\text{mol m}^{-2}\text{s}^{-1}$	7	2	↗	5/6 → 12
	7	2	→	4
	7	2	→	11
	7	2		

Fig. 7.2d shows treatment codes (numbers 1-13) and the arrows represent the sequence of transfers after each treatment analysis. The codes 1-13 are:

- 1 = 3 weeks HPD



- 2 = 3 weeks LPD
- 3 = 4 weeks HPD, same plants as in 1
- 4 = 4 weeks LPD, same plants as in 2
- 5 = 3 weeks HPD, fully expanded leaf which was analysed after one week in LPD
- 6 = 3 weeks HPD, leaf which matured after one week transfer to LPD
- 7 = 3 weeks LPD, one week after transfer to HPD; analysis of fully expanded leaf
- 8 = 3 weeks LPD, leaf which matured after a week of transfer to HPD
- 9 = 5 weeks HPD, same plants as in 1
- 10 = 5 weeks HPD
- 11 = 5 weeks LPD
- 12 = 3 weeks HPD, 2 weeks LPD same plants as in 5 and 6
- 13 = 5 weeks HPD, same plants as in 3

#### 7.3.5 Extraction and determination of chlorophyll content

Even though virtually all methods for estimation of the chlorophylls depend upon their extraction from plant tissues, there is no single solvent or solvent mixtures that will remove the unaltered green pigments rapidly and quantitatively from all kinds of plants.

The solvents most suitable for extraction of chlorophylls from plant material are those miscible with water such as methanol, ethanol, acetone, and acetone + ethylacetate. These solvents permit the direct estimation of chlorophylls. (For details refer to Šesták 1971).

Absorption spectra show that in 80 % acetone, there are two principal peaks in the blue and red regions. The absorption maximum in 80 % acetone is 663 nm, and is shifted to the red in virtual absence of traces of water to around 680 nm (a wavelength which is particularly effective in photosynthesis). Moreover, aggregates of chlorophyll in concentrated solutions show a small shift to the red whereas crystalline specimens in concentrated solutions show a maximum peak at 740 nm.



However, in plant tissues, particularly in the thylakoid membrane, the absorption peak of chlorophyll a is much broader than in extracts of the same tissue in a solvent. This has been explained by supposing that chlorophyll exists in possibly five or more types of aggregated states such as might occur in a lipoprotein membrane structure. These different "forms" are distributed between 664 nm and 703 nm, the principal component absorbing at 678-680 nm. These absorption maxima are not caused by other pigments other than chlorophyll a and the differences are physical, not chemical (Gregory, 1977).

For chlorophyll b, the band is in the red and occurs at 645 nm in 80 % acetone and is half the intensity, whilst the blue absorbing peak is slightly higher and shifted to the red. Chlorophyll b accompanies chlorophyll a in green algae and higher plants, except for mutant forms.

In this chapter, 6-10 leaves from each of the plant species and growth conditions (HPD and LPD) were excised and half the leaf area was used for chlorophyll extraction and determination. The other half was put in the oven for 24 hours at 90 °C for dry weight and specific leaf area determinations. Division of the leaf into two halves was along its axis of symmetry, so that two identical halves on an area basis were obtained.

The leaf material for chlorophyll pigment extraction was macerated with a small volume of 80 % acetone in a pestle and mortar. Using a little sand, the leaf material was crushed and ground in the normal way. The extract for chlorophyll determination was spun using a bench centrifuge for 3 minutes. Avoiding direct light, the extract was then diluted with a further 80 % to a known volume and this was put into the spectrophotometer (SP 800, Unicam, Sweden).



Chlorophyll concentration was calculated from the absorbance values using the equation of Ziegler and Egle (1965) quoted by Šesták (1971). These are in  $[\text{mg l}^{-1}]$ :

$$\text{Chlorophyll a} = 11.78 A_{664} - 2.29 A_{647}$$

$$\text{Chlorophyll b} = 20.05 A_{647} - 4.77 A_{664}$$

$$\text{Chlorophyll (a + b)} = 7.01 A_{664} + 17.76 A_{647}$$

where A is the absorbance at the wavelength.

The following parameters were recorded: Volume of 80 % acetone used, absorbance at 647 and 664 nm, dry weight and leaf area. Leaf area in  $\text{cm}^2$  was estimated using the leaf area meter (LI-1300 Li-Cor, Nebraska).

## 7.4 Results

### 7.4.1 Germination in the Fisons growth cabinet

Of the ten species under HPD and LPD in the Fisons growth cabinet conditions, only *Triplochiton scleroxylon* germinated in both conditions (Fig. 7.2b) *Terminalia ivorensis* and *Cyperus papyrus* germinated under HPD only.

Germination period and percentages in the growth cabinet varied :

(i) *Triplochiton scleroxylon* germinated 5 days after sowing under both HPD and LPD conditions; by the end of two weeks, germination percentages were 16 % and 23 % respectively.

(ii) *Terminalia ivorensis* started germinating two weeks after sowing under HPD, and only 10 % germination was recorded by 23/3/83.

(iii) *Cyperus papyrus* germinated under HPD and 5 days after sowing only



15 seedlings were available out of a few hundred seeds. These seedlings were not enough for experimental purposes.

#### 7.4.2 Germination under glasshouse mist bench conditions

(i) Under these conditions, *Triplochiton scleroxylon* reached 60 % germination, one week after sowing (Fig. 7.2c).

(ii) Germination in *Terminalia ivorensis* started 6 weeks after sowing and by the 9th week, 19 % germination was recorded.

(iii) By the 4th week after sowing, 100 % germination was recorded in *Terminalia superba* (Fig. 7.2 a).

(iv) Within 10 days of sowing, 70 % germination was recorded in *Khaya senegalensis* (Fig. 7.2d).

(v) One week after sowing, germination in *Cyperus papyrus* was still low.

(vi) The other seed species: *Khaya ivorensis*, *Chlorophora excelsa*, *Maesopsis eminii*, *Entandrophragma angolense* and *Nauclea diderrichii* had lost their viability.

#### 7.4.3 Specific leaf area and chlorophyll content

##### 7.4.3.1 The effect of light regime on specific leaf area and chlorophyll levels

The leaves grown at low photon flux density displayed much higher specific leaf areas than those grown in bright light (Fig. 7.3). This effect was evident in all species but especially pronounced in *Terminalia superba* (Fig. 7.3).

When chlorophyll levels are compared on a weight basis (Fig. 7.3), it is evident that leaves grown in dim light develop more chlorophyll,



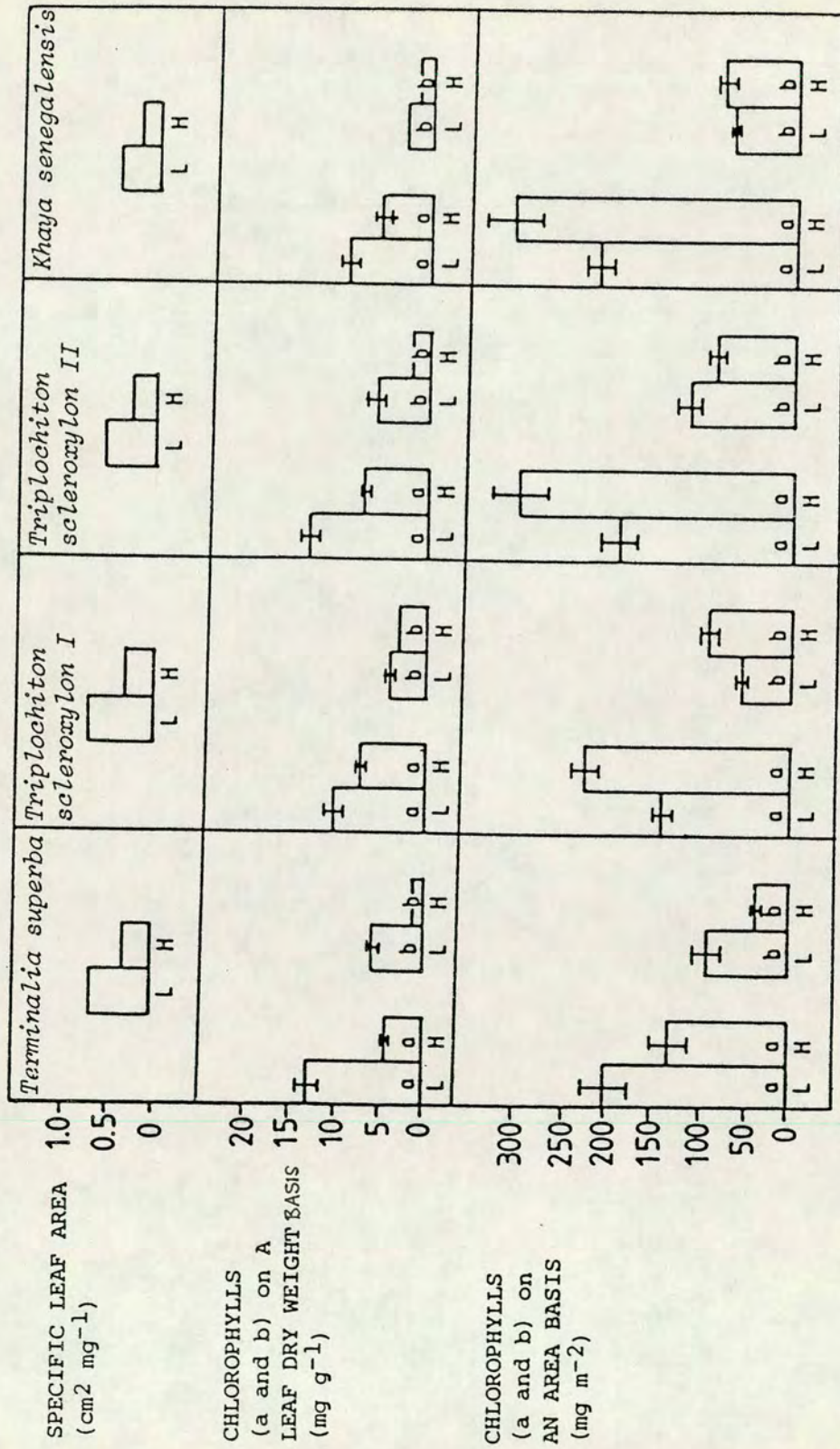


FIGURE 7.3: Effect of growth at low (L) and high (H) photon flux density ( $\approx 40$  and  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  respectively) on specific leaf area and chlorophyll  $\bar{a}$  and  $\bar{b}$  content expressed on both an area and dry weight basis.



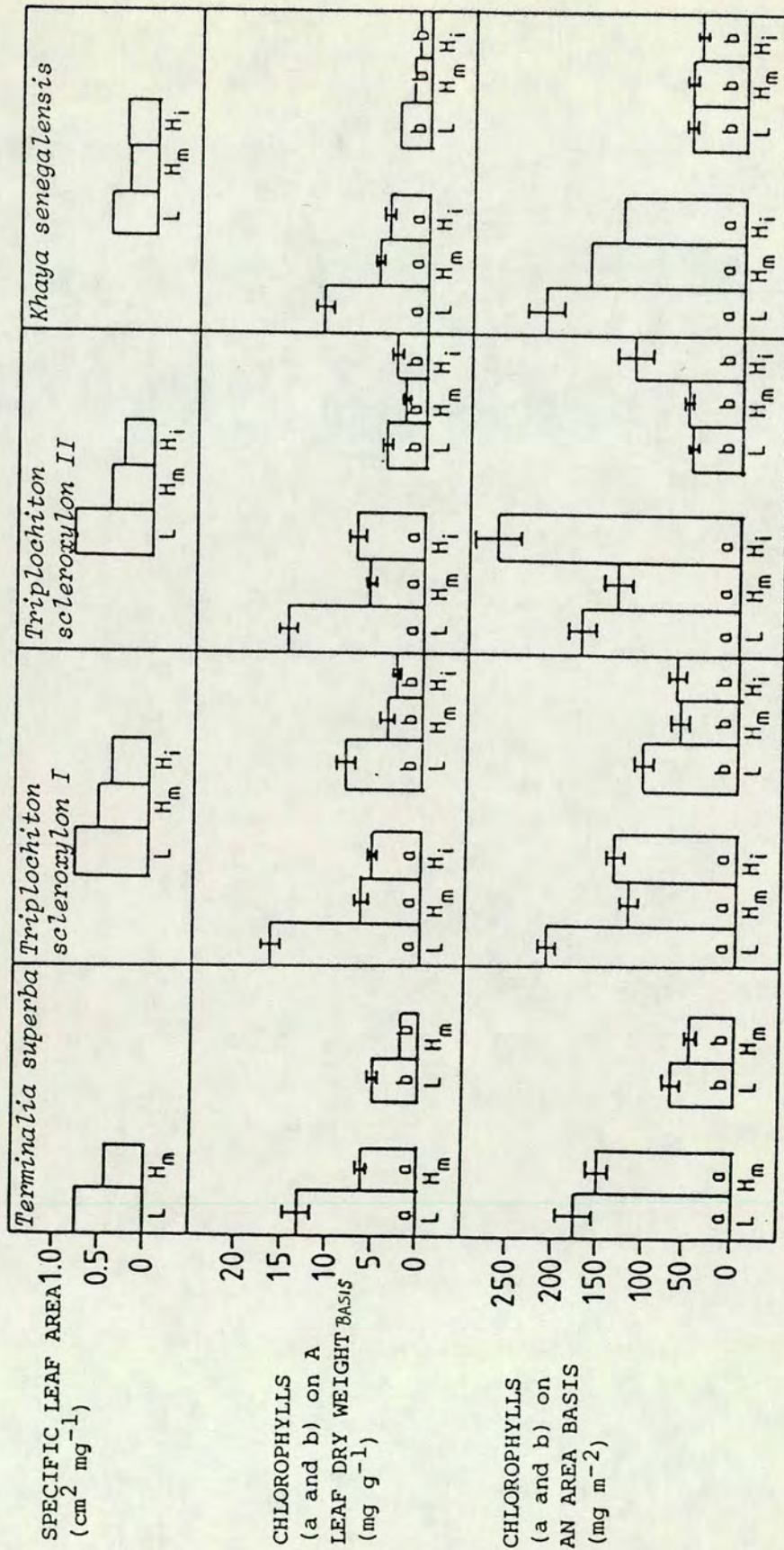


FIGURE 7.4: The effect of growth at low photon flux density (L) and subsequent transfer to high photon flux density (H) of mature leaves (H<sub>m</sub>) and immature leaves (H<sub>i</sub>) on specific leaf area and chlorophylls a and b content expressed on a leaf dry weight and an area basis.



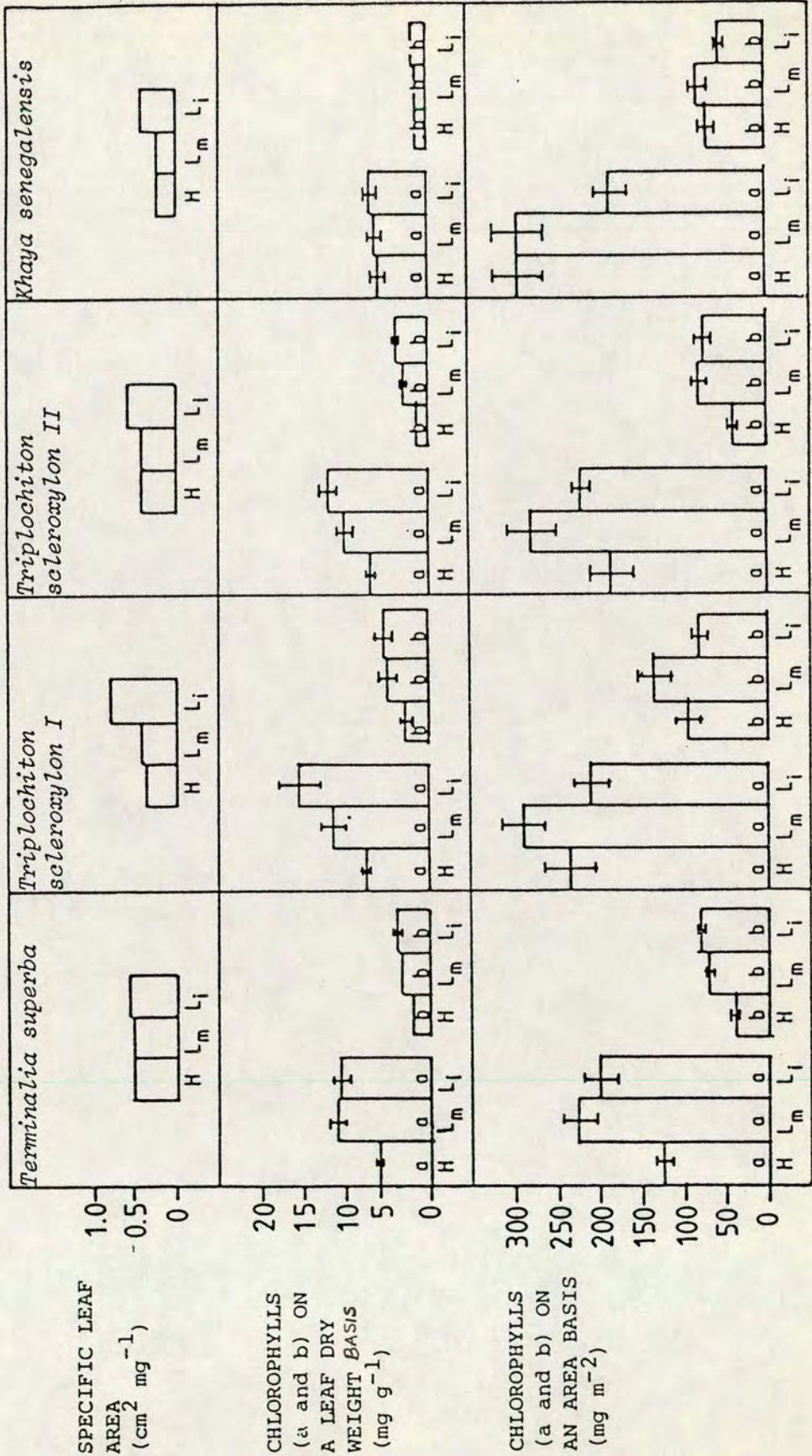


FIGURE 7.5: The effect of growth at high photon flux density (H) and subsequent transfer to low photon flux density (L) of mature leaves (L<sub>m</sub>) and immature leaves (L<sub>i</sub>) on specific leaf area and chlorophylls a and b content expressed on a leaf dry weight and an area basis.



and that this effect also is more pronounced in *Terminalia superba* (Fig. 7.3).

On an area basis it is only *Terminalia superba* that develops a higher chlorophyll content when grown in dim light (Fig. 7.3).

Chlorophylls a and b are influenced disproportionately by the light regime: usually the a/b ratio was increased by growth at high photon flux density (Fig. 7.3). This effect also was particularly pronounced in *Terminalia superba*.

#### 7.4.3.2 The effect of transfer from low to high photon flux density

On transfer from low to high photon flux density the specific leaf area declined (Fig. 7.4). This effect was more complete when the transfer took place during the period of leaf expansion. (It is perhaps surprising that any effect at all was observed when the transfer took place after the leaves were already fully expanded).

When chlorophylls are compared on a weight basis there is a sharp decline after one week. The new levels were similar to those which were observed when the leaf had developed entirely at high photon flux density (compare Fig. 7.4 with Fig. 7.3).

On an area basis the transfer to high photon flux density usually caused a decline in chlorophyll levels (Fig. 7.4).

#### 7.4.3.3 The effects of transfer from high to low photon flux density

When the leaves which were partially or completely expanded at high photon flux density were transferred to dim light the specific leaf area increased (Fig. 7.5). When this was assessed on leaves that were partially expanded, the specific leaf areas were similar in magnitude to those observed when the leaves developed entirely in dim light (compare Fig. 7.5 with Fig. 7.3).

On a weight basis the chlorophyll levels increased, in just one



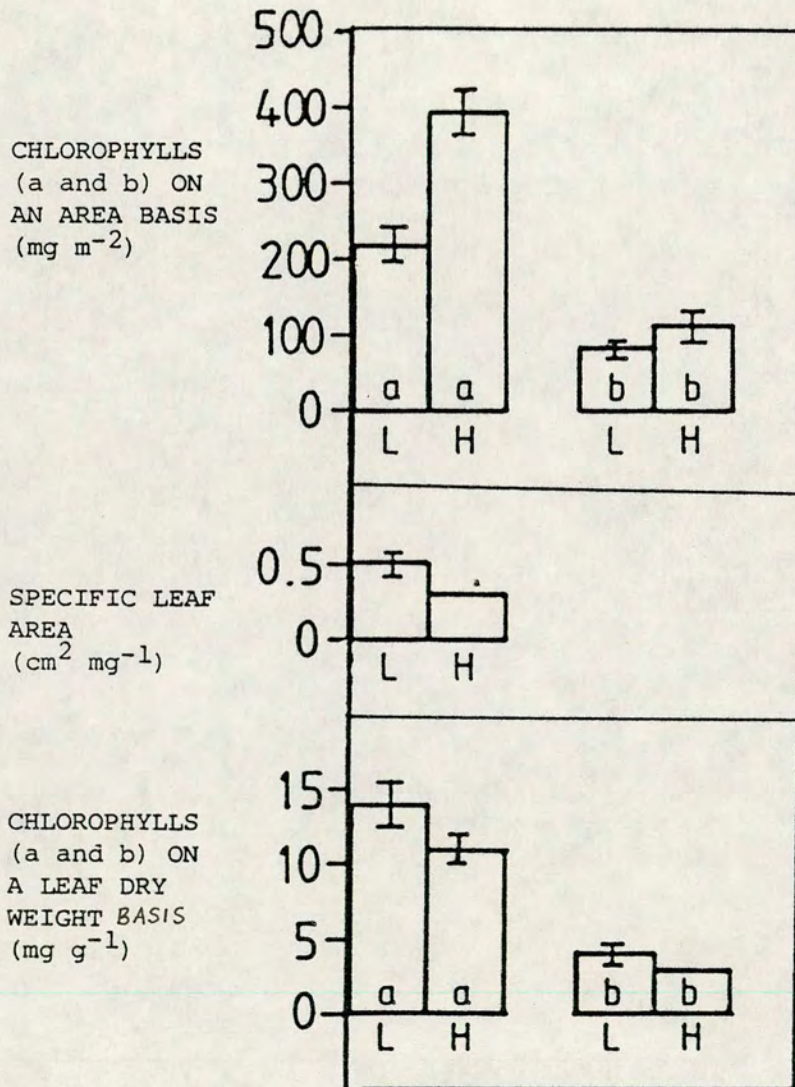


FIGURE 7.6: Effect of growth at Low (L) and high (H) photonflux density for one week on specific leaf area and chlorophylls (a and b) in *Cyperus papyrus* seedlings.



week, to values approaching those observed when leaves were developed entirely in dim light (compare Figs. 7.5 and 7.3).

On an area basis, it was only in *Terminalia superba* that consistent increases in chlorophyll levels were caused by the transfer.

#### 7.4.3.4 *Terminalia ivorensis* and *Cyperus papyrus*

*Terminalia ivorensis* was not considered due to irregular and poor germination.

*Cyperus papyrus* behaved rather differently from the tree species. On an area basis it developed maximum chlorophyll content under HPD not LPD (Fig. 7.6). Its reactions to step-wise changes cannot be reported as the HPD to LPD transfer caused plants to die. The LPD to HPD transfer was not attempted as the material raised under LPD was considered too depauperate for experimental purposes. Clearly *Cyperus papyrus* is not at all adapted for survival in dim light whereas all the tree species, to some extent, are able to tolerate these conditions.

#### 7.4.3.5 Other information regarding plant age

(1) In all species, SLA was higher at LPD than at HPD and it declined with leaf age (compare 3rd week with 4th week at either LPD or HPD).

(2) Chlorophyll a/b ratio was generally higher at HPD than LPD. It declined with plant age in *Triplochiton scleroxylon* I and *Khaya senegalensis*, but this tendency was not clear-cut in *Terminalia superba* and *Triplochiton scleroxylon* II.

(3) There were no significant changes in chlorophyll (a + b) content on an area basis in *T. superba* and *K. senegalensis* as a result of an extra week in LPD or HPD. However, it declined in *Triplochiton scleroxylon* I



at 4 weeks LPD whilst in *Triplochiton scleroxylon* II it increased by the 4th week in both LPD and HPD.

(4) On a leaf dry weight basis, chlorophyll (a + b) content was higher at LPD than HPD. It either declined or showed no significant changes between the 3rd and 4th week in both LPD and HPD.

## 7.5 Discussion

### 7.5.1 Evaluation of experimental conditions

The light climate, in terms of photon flux, was quite close to natural conditions of open sunlight or forest shade (e.g. Pearcy 1983; Chazdon and Fetcher 1984). No attempt was made to simulate diurnal cycles, and so the total daily flux of photons in these experiments was possibly rather more than that in natural conditions. On the other hand, maximum open values ( $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) were not obtained in the growth cabinet (see Fig. 7.1).

The step-wise change that was imposed does have parallels in the real forest environment. LPD→HPD→LPD occurs in sunflecks, but over a very short duration (minutes or hours), and involves a change in magnitude of up to 200 times. This requires that photosystems should be capable of harvesting photons from a wide range of flux densities without photoinhibition as a consequence of over-energization of the photosynthetic reaction centres.

LPD→HPD occurs during the processes of natural gap formation when trees fall or are felled (e.g. selective logging) as part of a management exercise, and when young plants raised in the nursery shade are planted in the open during afforestation and reforestation.

No attempt was made here to simulate the red/far-red ratios of the forest. This subject is addressed in Chapters 6 and 10. It should be recognised that low photon flux coupled with low R/FR may have additional effects to those outlined here.



### 7.5.2 Chlorophyll levels and chlorophyll a to b ratio

The chlorophyll (a + b) content of these tropical tree species was within the range of other  $C_3$  species reported in the literature. Also, the differences between these tree species in chlorophyll content were not large and depended mainly on whether the leaves were grown under LPD or HPD. Chlorophyll (a + b) content varied from 132 to 424  $\text{mg m}^{-2}$  on an area basis whilst on dry weight basis it varied from 5.3 to 20.9  $\text{mg g}^{-1}$ . Other species investigated (e.g. Masarovičová and Eliáš 1980; Morales *et al.*, 1982) showed similar values to those reported in this experiment. According to Šesták (1971), normal leaves contain 100–1000  $\text{mg m}^{-2}$  of chlorophyll (a + b) content. In a recent review by Björkman (1981) the average chlorophyll content for 49 sun and shade plants grown under a wide range of light regimes, was 485  $\text{mg m}^{-2}$ . He also pointed out that high chlorophyll content appears to be especially frequent among evergreen shade plants native to tropical forests (e.g. *Cordyline rubra*); but in this experiment, the tropical tree seedlings and the sedge did not differ in chlorophyll content from other species reported in the literature.

### 7.5.3 Development in low or high photon flux density

In natural forests, seedlings and saplings beneath a canopy of vegetation experience low photon flux density all the time except where gaps allow in sunflecks. It is generally known that the leaves of such shaded plants are thinner and their chloroplasts larger and richer in chlorophyll content than leaves of sun plants. Higher specific leaf area in leaves developed under LPD versus HPD is a major way in which the plant can adapt its growth to cope with the prevailing light regime.

However, once a leaf is fully expanded, it does not change its leaf area or number of cells. So this method of adaptation is limited to the conditions that prevail during leaf development. Subsequently, adaptation can only be achieved substantially by chlorophyll or structural and other anatomical changes leading to alterations in leaf



TABLE 7.2

Growth Period	Parameters recorded	<i>Terminalia superba</i>	<i>Triplochiton sclerocylon I</i>	<i>Triplochiton sclerocylon II</i>	<i>Khaya senegalensis</i>
3 weeks LPD	Chlorophyll(a+b)mg m <sup>-2</sup>	246 ± 25	316 ± 20	230 ± 20	282 ± 21
	SLA cm <sup>2</sup> mg <sup>-1</sup>	0.73 ± 0.03	0.78 ± 0.03	0.85 ± 0.05	0.52 ± 0.02
	Chlorophyll(a+b)mg g <sup>-1</sup>	17.9 ± 2.0	24.6 ± 1.7	19.4 ± 1.7	14.6 ± 0.8
	Chlorophyll a/b	2.62 ± 0.24	2.08 ± 0.09	3.26 ± 0.08	3.63 ± 0.21
4 weeks LPD	Chlorophyll(a+b)mg m <sup>-2</sup>	288 ± 36	196 ± 16	353 ± 28	284 ± 19
	SLA cm <sup>2</sup> mg <sup>-1</sup>	0.64 ± 0.02	0.72 ± 0.04	0.54 ± 0.04	0.41 ± 0.02
	Chlorophyll(a+b)mg g <sup>-1</sup>	18.1 ± 1.8	14.0 ± 1.3	18.9 ± 1.7	11.9 ± 1.1
	Chlorophyll a/b	2.3 ± 0.24	2.6 ± 0.09	2.19 ± 0.12	3.18 ± 0.11
3 weeks HPD	Chlorophyll(a+b)mg m <sup>-2</sup>	164 ± 14	327 ± 43	229 ± 32	364 ± 65
	SLA cm <sup>2</sup> mg <sup>-1</sup>	0.48 ± 0.02	0.34 ± 0.03	0.39 ± 0.03	0.23 ± 0.02
	Chlorophyll(a+b)mg g <sup>-1</sup>	7.8 ± 0.05	10.5 ± 1.1	8.4 ± 0.6	7.6 ± 1.0
	Chlorophyll a/b	3.31 ± 0.06	2.63 ± 0.17	4.44 ± 0.14	4.29 ± 0.24
4 weeks HPD	Chlorophyll(a+b)mg m <sup>-2</sup>	165 ± 25	319 ± 21	384 ± 37	390 ± 60
	SLA cm <sup>2</sup> mg <sup>-1</sup>	0.32 ± 0.01	0.33 ± 0.02	0.25 ± 0.02	0.18 ± 0.1
	Chlorophyll(a+b)mg g <sup>-1</sup>	5.2 ± 0.8	10.1 ± 0.5	9.3 ± 0.8	6.9 ± 0.8
	Chlorophyll a/b	4.0 ± 0.28	2.51 ± 0.14	3.35 ± 0.11	3.81 ± 0.24

Shows the effect of 3 - 4 weeks growth at either LPD or HPD on chlorophyll (a+b) content on both an area and dry weight basis, SLA and chlorophyll a/b ratio. ± standard error.



thickness. Besides, chlorophyll accumulation per unit leaf matter usually stops prior to reaching maximum leaf area, or soon thereafter (Masarovičová and Eliáš, 1981). Afterwards, the chlorophyll content per area and weight declines (Šesták, 1977). In this experiment, Fig. 7.5 shows that transfer of fully expanded leaves to LPD for a week resulted in increased chlorophyll synthesis although specific leaf area remained only a little higher than in the leaves that had been under HPD.

In addition to the specific leaf area being dependent on the light regime, the chlorophyll content per weight of leaf material is also dependent on the light regime during growth. In all cases the chlorophyll (a + b) content in  $\text{mg g}^{-1}$  was higher at LPD than at HPD. There is a tendency for the chlorophyll a/b ratio to be higher in HPD than in LPD leaves. Boardman (1977) noted that if chlorophyll content was expressed as per unit leaf area, it was frequently lower in shade species and shade leaves. Lewandowska and Jarvis (1977) showed on a leaf area basis that there were no significant differences between chlorophyll content in Sitka spruce because of the compensating variations in specific leaf area. Moreover, Eliáš (1979) showed that variations in specific leaf area within a forest canopy were large; and this also concerned the leaves in various parts of the crown.

Chlorophyll a/b ratio varied between 1.84 - 5.0 in this experiment. Under HPD it was higher than that at LPD. Šesták (1971) reported that the chlorophyll a/b ratio for normal leaves is generally between 1.5 to 3.0. Masarovičová and Eliáš (1981) found that this ratio was usually above 3.0 for sun leaves and often below 3.0 in shade leaves; they suggested that this ratio might be a good leaf characteristic for expressing interspecific differences and adaptability of plants to irradiance. In this experiment, chlorophyll a to b ratio varied with the light regime during the leaf development and declined slightly with leaf age in some species (see Table 7.2).

Higher chlorophyll a/b ratio under HPD than in leaves grown at LPD is thought to be related to leaf anatomy. It is generally stated that chloroplasts in shade leaves are larger and richer in chlorophyll b



relative to chlorophyll a than in sun leaves (e.g. Björkman and Holmgren 1963; Björkman 1968); and that shade-adapted leaves have a greater number of chloroplasts in the mesophyll cells, adjacent to the upper leaf surface than sun-adapted leaves (Goodchild *et al* 1972). These distinctions are well known and have been observed in sun and shade leaves of many species, as well as in single species when grown at low or high photon flux densities (e.g. in the review by Boardman, 1977). In addition shade leaves usually have lower contents of soluble protein and a corresponding lower soluble protein to chlorophyll ratio than sun leaves (e.g. Björkman 1968; Goodchild *et al* 1972). Moreover, shade plants show a greater degree of grana formation than sun plants. It is believed that grana thylakoids contain a lower chlorophyll a/b ratio than do stroma lamellae (e.g. Park and Sane, 1971). Anderson *et al.*, (1973) related the extent of grana formation in shade plant chloroplasts to their total chlorophyll (a + b) content and suggested that grana formation may be the means of achieving a higher density of light harvesting pigment assemblies and hence a more efficient collection of light quanta. However, the lower chlorophyll a/b ratio of shade leaves does not appear to be due to a significant increase in the ratio of photosystem II to photosystem I (e.g. Boardman, 1977). Higher chlorophyll content per unit leaf area in shade plants is thought to be strongly related to the higher quantum efficiency rather than greater absorption of light energy. Moreover, the reduction in the quantum efficiency of shade plants when grown under strong light (HPD) is not attributable to chlorophyll destruction *per se*, but to the loss of photosystem II which is more sensitive to HPD than photosystem I (Björkman, 1968).

In this experiment, the result of transfer from LPD to HPD was chlorophyll decomposition (Fig. 7.4). Damage to the light harvesting system can be either photo-oxidation or photoinhibition.

Available evidence in the literature suggests that photoinhibition is caused by an inactivation of the reaction centres of photosystems from the light harvesting pigments, and that shade plants have an intrinsically low potential for photosynthetic light acclimation. It seems likely that their high susceptibility to high light injury is largely a



consequence of their inherent low ability to increase their capacity for effective utilization of high quantum flux densities for photosynthesis (e.g. Björkman 1981; see also Chapter 9 of this thesis). The results of this experiment suggest that all the tree species investigated did just as well, and there was no difference between those thought as light demanders or shade tolerators.

More evidence, e.g. Björkman (1968) shows that failure of shade clones of *Solidago virgaurea* to adapt to high light levels is associated with a low capacity of such plants to increase the level of ribulose-1-5-bisphosphate carboxylase and perhaps also other components which potentially determine the capacity for light saturated photosynthesis. This was confirmed by Gauhl (1969, 1970) and many other research workers in this field. For detailed information, refer to the recent review by Björkman (1981). This aspect is outside the scope of this thesis.

Nevertheless, all the species investigated in this experiment showed a high degree of adaptation to step-wise changes in photon flux density. This adaptation to step-wise changes in photon flux density ties in very well with the fact that chlorophyll synthesis and decomposition are continuous in the leaves, and that synthesis and breakdown of carboxylation enzymes depend on the light climate. The rates of these processes may be important in adaptation to different light climates. Besides, an increase in chlorophyll content may confer a significant advantage under conditions where photon flux density is very low and severely limits the photosynthetic rate.

#### 7.5.4 Response of specific leaf area to a step-wise change

On transfer from low to high photon flux density, the photosystem that is adapted to harvest  $40 \mu\text{mol m}^{-2} \text{s}^{-1}$  is subjected to what is presumably an enormous overload (25 times greater). Chlorophyll content changes that occur consequently may be interpreted as destruction or orderly re-adaptation. The data suggest an orderly re-adaptation, as the new chlorophyll values on a dry weight basis (Fig. 7.4) are very close to the values that were found in the leaves which



had developed all the time at HPD (e.g. Fig. 7.3). There is even some evidence that the specific leaf area of a fully expanded leaf adapts too, though this is more likely to reflect a large loading of the leaf with starch and other products of an increased rate of photosynthesis or, as reported earlier, structural changes such as thickening of the mesophyll cells, besides changes in the chloroplast morphology. Altogether these could account for specific leaf area decreases. However, if we assume that changes were brought about by chemical changes in the leaf, for instance starch synthesis: on a dry weight basis starch content of leaves can be, in the extreme, as high as 20 % and soluble sugars can be a further 10-15 %. So altogether, 1g of 'starved' leaf at LPD could become 1.35 g of leaf at HPD without need to postulate any other kinds of change. This would lead to a change in apparent chlorophyll of  $X/1$  to  $X/1.35$ , which is a 26 % decline. The observed declines are usually greater than this calculated value :

<i>Terminalia superba</i>	44 %
<i>Triplochiton scleroxylon</i> I	22 %
<i>Triplochiton scleroxylon</i> II	47 %
<i>Khaya senegalensis</i>	40 %

Thus, the data suggest some degree of adaptive change in specific leaf area, though the nature of this change is at present unknown.

Transfer of fully expanded leaves in the opposite direction, HPD to LPD resulted in hardly any significant changes in specific leaf area at all; leaves are thus operating at LPD with specific leaf area which is characteristic of HPD.

#### 7.5.5 Ecological evaluation

All tree species displayed adaptability, but the  $C_4$  sedge behaved quite differently (Fig. 7.6). The ecological characteristics of the



species suggest that *Terminalia superba* (Lamb and Ntima, 1971) and *Triplochiton scleroxylon* (Onyeagocha, 1962) are light demanders. The ranking in order of light demanders->shade tolerator is in the sequence: *Terminalia superba*>*Triplochiton scleroxylon*>*Khaya senegalensis*. However, there is no clear-cut indication of this sequence in the data on the basis of chlorophyll content or specific leaf area. Indeed *Khaya senegalensis* displays the lowest specific leaf area, a feature which might be considered disadvantageous for light harvesting in the dim layer. On the other hand, a low specific leaf area is consistent with the view that the leaves may be organs of storage in this situation, being thicker.

The two sowings of *Triplochiton scleroxylon* behaved somewhat differently. Plants from the second sowing developed higher chlorophyll levels and lower specific leaf areas. This variation within a batch of seeds could have resulted from rather different selection pressures operating at germination and establishment phases.

Finally, as regards specific leaf area, in the real forest situation, dominant species in the upper storey may have some leaves exposed to direct sunlight whilst others are shaded. From an early age, these species show an adaptation especially in specific leaf area, as variations occurred within a species as a result of development at either HPD or LPD. Perhaps all trees to some extent are adaptable to shade in this respect.



## CHAPTER EIGHT

## MEASUREMENT AND INTERPRETATION OF GAS EXCHANGE

The main techniques of measuring the carbon balance and gas exchange of plants have been reviewed by Šesták, Čatský & Jarvis (1971) and include growth analysis, radioactive tracers and net carbon dioxide and oxygen exchange.

The technique of growth analysis was used in the investigation of the effects of glasshouse shade (Chapter 5) and reduced photon flux density, with a low or high red/far-red ratio (Chapter 6), on the carbon balance of *Khaya senegalensis* and *Terminalia ivorensis*. Also, in the previous chapters, it was shown that shade had significant effects on net assimilation rate (Chapter 5), that R/FR influenced leaf development (Chapter 6), and that chlorophyll content was affected by the photon flux density during leaf development (Chapter 7). In this chapter is described the methods that have been used for measuring  $\text{CO}_2$  and water vapour exchange rates, and the approach adopted in the analysis of data from plants under various shade conditions as described in Chapters 9 and 10.

Analysis of plant responses to shade requires, as a minimum, a method of measuring the rate of photosynthesis under controlled conditions. If at the same time, water vapour exchange is measured, then it is possible to investigate the  $\text{CO}_2$  transfer resistances as first shown by Gaastera (1959). He showed how the transpiration rate could be used to evaluate the stomatal resistance,  $r_s$ ; and how this resistance could then be applied to the measured rate of photosynthesis to derive a quasi-resistance,  $r_m$ ; the mesophyll resistance. His studies paved the way for much following work, including resistance analogues for transfers within canopies of crops (for an up-to-date résumé, see Jones 1983).

In recent years, more sophisticated models of photosynthesis have been fitted to data sets, describing the entire response curve and



revealing still more information about the photosynthetic process (Goudriaan 1978).

### 8.1 Measurement of CO<sub>2</sub> and water vapour exchanges

Reviews of the literature on gas exchange techniques have been presented by Šesták *et al.*, (1971) and Coombs and Hall (1982). Nearly all CO<sub>2</sub> analysers produce accurate results given adequate precautions, but they differ greatly in expense, portability, range of parameters measured, sample handling capacity, and experience required for accurate measurements: no single instrument represents the best solution for all gas-exchange problems (Field and Mooney, 1984).

The commonest technique involves measurements of net gas exchange in cuvettes that range in size from small ( $\approx 1 \text{ cm}^3$ ) single leaf chambers for portable porometer to large ( $> 10 \text{ m}^3$ ) chambers that enclose whole plants or areas of plant canopy. The degree of environmental control in these cuvettes can vary in sophistication up to completely independent control of temperature, light, humidity and CO<sub>2</sub> partial pressures in the best laboratory systems (Jones, 1983).

The most usual method for CO<sub>2</sub> detection is the use of the infra-red gas analyser (IRGA) that makes use of strong CO<sub>2</sub> absorption in the infra-red region of the spectrum especially at  $4.26 \mu\text{m}$  (see Jones 1983 p.21). The radiation from an infra-red source passes through a fixed-volume analysis cell, containing the sample gas, to a detector, and the absorptance depends on the number of molecules of CO<sub>2</sub> in the optical path. Cross sensitivity to other atmospheric gases (especially water vapour which has a common absorption band with CO<sub>2</sub> at  $2.7 \mu\text{m}$ ) can be eliminated by use of interference filters to restrict sensitivity to approximately  $4.3 \mu\text{m}$  absorption band.

In this study, carbon dioxide and water vapour exchanges were determined using a LI-1600 steady-state porometer (LiCor- Nebraska) and a Binos infra-red gas analyser (IRGA, Binos 2-Leybold Heraeus, London) together. This combination consisted of the porometer linked to the



Binos in a semi-closed system, so that  $\text{CO}_2$  and water vapour exchange of the leaf could be determined concurrently (see Fig. 8.1).

### 8.1.1 Description of the equipment: the LI-1600 Steady-State Porometer

Accurate measurements are essential for any study of gas exchange in either the laboratory or the field. For most leaves, the largest part of gaseous flux is through the stomatal pore, and consequently leaf conductance after allowance of the boundary layer, can generally be regarded as almost synonymous with stomatal conductance (Jarvis, 1981). Nowadays, leaf or stomatal conductance is measured with diffusion porometers. The majority of these porometers are similar in principle and have been described by several authors (e.g. Kanemasu *et al.* 1969, Parkinson and Legg 1972, Beardsell, Jarvis and Davidson 1972, Körner and Cernusca 1976, Bingham and Coyne 1977; and Jarvis 1981).

According to Jarvis (1981) there are essentially three basic designs of porometers in use and they all embody a small chamber which is attached to part of a leaf or which encloses one or more leaves. These are :

- (1) the unventilated 'transit-time' type
- (2) the ventilated 'transit-time' type
- (3) the ventilated 'steady-state' type.

In this study, the ventilated steady-state porometer was used. This porometer is a commercial design developed using the null balance principle of Beardsell *et al.*, (1972). In addition to the features of the original instrument, this one incorporates its own microprocessor with sensors for leaf temperature, chamber temperature, relative humidity and quantum flux; so that both transpiration and stomatal conductance are computed by the microprocessor and displayed directly.

Water loss from the leaf is determined by maintaining a constant



vapour density in the chamber that is in contact with the transpiring leaf. This is achieved by pumping dry air into the chamber (porometer cuvette) at an appropriate, measured rate to obtain a balance at which the humidity inside the chamber neither rises or falls.

The operation of this porometer requires setting the leaf area which depends on the type of leaf and in turn the head used on the cuvette. In all cases where the sample covers the entire aperture, read out of  $r_s$  is direct. The LI-1600 porometer assumes a fixed boundary layer resistance ( $r_a$ ) of  $0.15 \text{ s cm}^{-1}$ . Stomatal conductance is then determined from tables of saturation vapour density vs temperature which are stored in LI-1600 memory. This relationship is used in the calculation of water vapour density of the dry air stream entering the cuvette.

The porometer also has a quantum sensor attached to the chamber which measures photosynthetically active radiation (PAR) incident on the leaf within the chamber (400-700 nm).

However, the LI-1600 porometer, like other porometers is subject to errors arising from :

- 1) Changes in calibration of the humidity sensor and flow meter
- 2) Thermal gradients within the chamber - particularly the leaf-to-sensor difference.

Hence, no single calibration procedure is infallible as errors arise from variations in operation (A.P.Sandford pers. comm.). For flat broadleaves, the errors are negligible in the LI-1600 porometer as long as care is taken in measuring the leaf temperature. Calibration was checked with the kit provided by the manufacturers, and the tubing system was checked to avoid any leakages in the gas flow systems.

#### 8.1.2 The Binos differential IRGA



The Binos IRGA in this experiment has been used and described comprehensively by Griffiths and Jarvis (1981) and Griffiths (1983). It is a two-channel instrument with absolute and differential gas paths and optics measuring  $\text{CO}_2$  concentrations. The absolute channel has a sealed reference and a measuring range of 0 to  $500 \mu\text{mol mol}^{-1}$ , whilst the differential has a flowing gas path and measuring range of  $\pm 50 \mu\text{mol mol}^{-1}$ . Both channels have optical and gas filters to selectively measure absorption at  $4.3 \mu\text{m}$  and thus reduce cross-sensitivity between  $\text{CO}_2$  and water vapour (see Šesták *et al.*, 1971). However, slight cross-sensitivity remained, so that a correction factor had to be used (see below).

The instrument is calibrated periodically using gas mixing pumps. For details of its operation, tests and calibration, refer to Griffiths and Jarvis (1981).

In conjunction with the Binos IRGA, a chart recorder (Servoscribe 220, Smith Industries Ltd., U.K.) was connected to follow the trends in  $\text{CO}_2$  exchange of the leaf.

### 8.1.3. The flow system

The semi-closed gasometric principles followed are those described by Jarvis and Čatský (1971), and the flow system is that shown in Fig. 8.1 and described below.

Outside ambient air ( $\approx 340 \mu\text{mol mol}^{-1}$  of  $\text{CO}_2$ ) was sucked by a pump in the LI-1600 porometer into four, 10-litre buffer tanks. These buffer tanks served as reservoirs to damp down any fluctuations in the ambient  $\text{CO}_2$  concentration. The air then passed through fresh silica-gel to remove water vapour and also to further damp out  $\text{CO}_2$  concentration fluctuations.

Using Viton tubing (Mitsui TPX, Surrey U.K); one flow line went through the porometer into the chamber, and the other into the Binos IRGA differential port to act as a reference line. A flow line into the porometer chamber was connected to the Binos differential sample



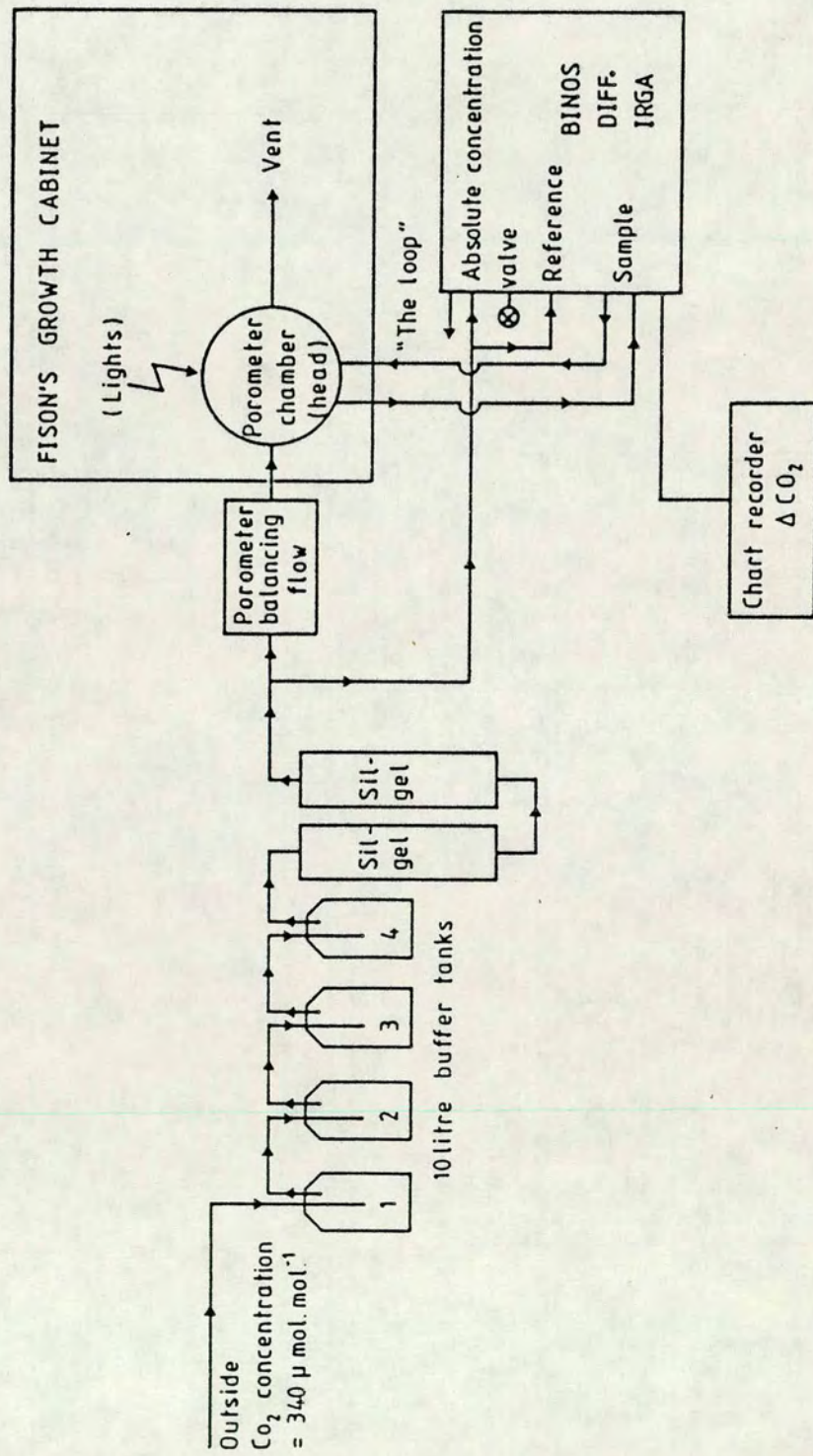


Fig.8.1 Diagrammatic block layout of the gas flow system.



channel in a closed-loop by two polypropylene tubes (3 mm internal diameter, 3 m long).

The changes in gas concentration of the air caused by the plant material was determined with the Binos IRGA through the analysis of the gas entering the reference air stream and that leaving the sample line. Thus, in the chamber, water vapour and  $\text{CO}_2$  exchanges occur between the leaf and the chamber air mainly due to transpiration and photosynthesis. This results in changes in vapour pressure and  $\text{CO}_2$  concentration in the sample air compared to that of the reference line. Ultimately, in the chamber there is an increase in water vapour which causes a small but appreciable dilution of the  $\text{CO}_2$  concentration irrespective of the rate of photosynthesis. Therefore, need for a correction arises as suggested by Parkinson (1971).

The flow rate was automatically regulated by the mass flow controller integral to the LI-1600 porometer control unit. This system found the flow rate of dry air required to balance the input of water vapour by transpiration, and the microprocessor calculated stomatal conductance.

When photosynthesis occurred, the  $\text{CO}_2$  concentration within the chamber decreased and this was displayed as a negative reading on the Binos differential channel until a steady state was reached. When respiration occurred in the "dark" the  $\text{CO}_2$  concentration increased and this was displayed as positive reading on the Binos differential channel. Final readings were taken when both the porometer flow rate and the Binos recordings reached a steady state.

#### 8.1.4 Neutral density glass filters

A set of 5 mm thick, 18 cm long and 9 cm wide neutral density glass filters (Frew-Smith Ltd., Irvine, Scotland) were used to vary the photon flux density incident on the leaf in the chamber. It was possible to obtain a range of photon flux density values up to  $700\text{--}1500 \mu\text{mol m}^{-2}\text{s}^{-1}$  at about 300–400 mm from the double glazed roof of the Fisons growth cabinet (section 7.2.2, Figure 7.1.). These



neutral density glass filters reduced the incident photon flux density by 50%, 25%, 12%, 5% and 1% respectively.

Darkness was obtained by covering the plant and the light sensor with a black polythene sheet.

#### 8.1.5 Test check of the flow system and correction factors

Whenever the carbon dioxide infra-red gas analyser (IRGA) is used to determine the photosynthesis and respiration rate of a leaf, there is some residual cross sensitivity to water vapour for which corrections must be made (Parkinson, 1971). Parkinson performed experiments on carbon dioxide gas analysers when the air was dried or not dried before analysis with or without interference filters.

(1) With IRGAs fitted with interference filters, the reference air is unmodified so the  $\text{CO}_2$  and water-vapour content is the same as the air entering the leaf chamber. However, the analysed air that passes through the leaf chamber is modified in its carbon dioxide concentration and water vapour content (E) due to the leaf photosynthesis and transpiration. Because of the added volume of water vapour (E) the volume of the air leaving the chamber ( $V_0$ ) is greater than that entering it ( $V_i$ ). Thus:

$$V_0 = V_i + E \quad 8.1$$

The analyser deflection is proportional to the difference between carbon dioxide and water vapour concentrations of the analysis and reference air streams.

(2) When air is dried before analysis, then the water vapour content of the reference and analysis air streams are both equal to zero, and hence there can be no instrument response to water vapour. Nevertheless leaf transpiration can still cause an error because the sample (analysis) air has had some water vapour added in the chamber by the leaf.



In this experiment, as described in the previous sections, the IRGA had an interference filter and the air was dried in silica-gel as shown in Figure 8.1. Nevertheless, to check the theoretical correction (derived by Parkinson, 1971) for the effect of transpiration on  $\text{CO}_2$  concentration and also test for the empirically derived cross-sensitivity (Griffiths, Unpub.) a simple test was performed.

A layer of wet filter paper was inserted in the chamber instead of the leaf. This was assumed to have zero  $\text{CO}_2$  exchange. The porometer was set to balance at  $21.4^\circ\text{C}$  and 50.4% relative humidity. This resulted in a balancing flow of dry air into the chamber of  $4.23\text{ cm}^3\text{ s}^{-1}$ , with a measured evaporation rate of  $199.8\text{ mg m}^{-2}\text{ s}^{-1}$ .

Using the equation given in section 8.1.7 this gave a calculated  $\text{CO}_2$  differential of  $-2.94\text{ }\mu\text{mol mol}^{-1}$ . The measured  $\text{CO}_2$  differential was  $-2.9\text{ }\mu\text{mol mol}^{-1}$ . Similar results were recorded for repeated tests. Bearing in mind the noise level of the Binos ( $\approx 0.5\text{ }\mu\text{mol mol}^{-1}$ ) and the error of determining cross-sensitivity, the correction thus seemed adequate. Errors in  $\text{CO}_2$  analysis of about  $1\text{ }\mu\text{mol mol}^{-1}$  are unimportant except at very low light levels and in the dark, when the recorded differential was only a few  $\mu\text{mol mol}^{-1}$ .

#### 8.1.6 Experimental procedure

(a) Every day the Binos IRGA was switched on around 0800 h. After about 15 minutes warm-up time, the porometer was switched on. The Binos was then tested for the zero reading of the differential channel. This was done by increasing the flow of dry air into the chamber to a maximum flow rate of  $10\text{--}12\text{ cm}^3\text{ s}^{-1}$  whilst the chamber was sealed, to remove any condensation in the tubing and the chamber. The chamber was sealed with a thick plastic film impermeable to  $\text{CO}_2$  and water vapour. The flow was then reduced to  $2\text{ cm}^3\text{ s}^{-1}$ , a typical flow in the experiments, and the Binos differential zero recorded.

(b) After 9.30 a.m. when the lights of the Fisons cabinet came on, the chamber was closed around the leaf to be investigated with a fixed leaf area of  $2\text{ cm}^2$  (for tree species) and  $1\text{ cm}^2$  (for papyrus). When



transpiration occurred, the relative humidity in the chamber increased. This was off-set by an automatic increase in flow, produced by the porometer, at such a rate as to return and maintain the relative humidity at the set point.

(c) A neutral density glass filter or black polythene sheet was then selected for the desired photon flux density and placed on top of the leaf chamber and the quantum sensor. A total of 7 readings for each leaf were recorded. Each reading was taken when steady-state  $\text{CO}_2$  and water vapour exchange was observed and recorded by the chart recorder. Then, stomatal conductance, flow rate, transpiration rate, leaf temperature, quantum flux, differential reading of  $\text{CO}_2$  as well as background  $\text{CO}_2$  concentration of the ambient air were recorded for calculation of photosynthesis rate.

Although  $\text{CO}_2$  flux may have stabilized, in order to achieve a steady - state at each photon flux density, essential for good determination of stomatal conductance, a period of 30-60 minutes was required and so only two plants could be studied each day.

#### 8.1.7 Calculation of the photosynthetic rate including corrections

The amount of  $\text{CO}_2$  taken up by the plant material was estimated from the difference in  $\text{CO}_2$  concentration of the air before and after it had passed through the assimilation chamber as described by Šesták, Čatský and Jarvis (1971).

The procedure adopted in these experiments is different from that of Griffiths and Jarvis (1981). They employed the null-balance principle not only for water vapour, but for  $\text{CO}_2$  as well. They bled into the assimilation chamber a measured flow of  $\text{CO}_2$ -enriched air until there was no difference in  $\text{CO}_2$  between incoming and outgoing air streams. After that they balanced for water vapour.

In the present work, the null-balance principle was used for water vapour, and the assimilation rate was measured as the difference in concentration of  $\text{CO}_2$  between the sample and reference lines at



whatever flow rate through the chamber happened to prevail.

It is becoming increasingly common and convenient to express flows and concentrations in molar form (e.g. Jones 1983, p.45).

The Ideal Gas Law states that:

$$PV = nRT, \quad 8.2$$

however, in terms of fluxes, it can be modified to

$$PV' = n'RT \quad 8.3$$

where

P is the atmospheric pressure (Pa or  $\text{J m}^{-3}$ )

V' is the volumetric flow ( $\text{m}^3 \text{s}^{-1}$ )

n' is the molar flow ( $\text{mol s}^{-1}$ )

R is the gas constant =  $8.314 \text{ J K}^{-1} \text{ mol}^{-1}$

T is the absolute temperature degrees Kelvin

Thus, the molar flow of dry air into the porometer chamber is

$$n'_i = \frac{P v'}{8.314T} \quad 8.4$$

The extra volume caused by transpiration (E) provides an additional flow for water vapour  $n'_e$  where:

$$n'_e = E.A \quad 8.5$$

and A is the leaf area in  $\text{m}^2$

E is in  $\text{mol m}^{-2} \text{s}^{-1}$



Thus, total flow out of the chamber in  $\text{mol s}^{-1}$  is

$$n'_t = n'_i + n'_e \quad 8.6$$

$n'_t$  is total flow out of the chamber

$n'_i$  is the flow of dry air in the chamber

$n'_e$  is additional flow of water vapour caused by transpiration of the leaf within the chamber.

This is the basis for a correction to allow for the effect of the transpirational component on the volume of the measured  $\text{CO}_2$  difference ( $\Delta x$ ). The corrected  $\text{CO}_2$  difference ( $\Delta x'$ ) is then:

$$\Delta x' = \Delta x + x_a (1 - n'_i/n'_t) \quad 8.7$$

where :

$\Delta x$  is the volume of  $\text{CO}_2$  in the sample line ( $\mu\text{mol mol}^{-1}$ )

$x_a$  is the ambient (reference)  $\text{CO}_2$  concentration as a molar fraction.

Then, a fixed correction must be applied, based on the test with the Binos IRGA under the conditions of the experiment, to allow for a residual cross-sensitivity of water of  $1 \mu\text{mol mol}^{-1}$  per kPa of water vapour. The saturated vapour pressure at  $30^\circ\text{C}$ , is 4.24 kPa and at 50 % R.H. this corresponds 2.12 kPa. Therefore, as the reference air is dry, then at  $50 \pm 2\%$  relative humidity and  $30^\circ\text{C}$ :

$$\Delta x' = (\Delta x - 2.12) + x_a (1 - n'_i/n'_t) \quad 8.8$$

The photosynthetic rate ( $F_n$ ) can thus be calculated using :

$$F_n = \frac{n'_t \cdot \Delta x'}{A} \quad 8.9$$



## 8.2 Data handling and analysis

After calculating net photosynthesis rate, experimental values of photon flux density and stomatal conductance were used in a mathematical model based on physiological principles underlying the interplay of the gas exchange parameters.

It was a primary aim to evaluate whether there were any differences in species response to the treatments viz-a-viz high or low (HPD and LPD) photon flux densities (Chapter 9) and different red/far-red (R/FR) ratios (Chapter 10).

### 8.2.1 Rectangular hyperbola

The response of photosynthesis to quantum flux density is commonly described as a rectangular hyperbola (e.g. de Wit 1965; Procter *et al.* 1976; Thorpe *et al.* 1978).

Many mechanistic models have been proposed for biochemical reactions of photosynthesis following Maskell's (1928) and Rabinowitch's (1951) pioneering applications of Michaelis-Menten kinetics (e.g. Lommen *et al.*, 1971; Hall 1979; Farquhar *et al.*, 1980b). In many, the carboxylation reaction has been assumed to be the main intercellular limitation to photosynthesis and to have a rectangular hyperbola kinetics. In some cases the saturation is so sudden that observed curves can approach the so called 'Blackman response' of two straight lines (a constant initial slope where photosynthesis is entirely  $\text{CO}_2$ -limited, switching suddenly to a horizontal light-limited portion) e.g. as shown by Thornley (1976). The wide range of these observed responses can, however, be described by a non-rectangular hyperbola (see Jones, 1983 p.158).

### 8.2.2 Non-rectangular hyperbola

The photosynthetic rate increases approximately linearly over low photon flux densities; this increase is followed by a gradual, but still substantial, increase over high photon flux densities until saturation is



reached and photosynthesis becomes independent of light.

Several people have used a non-rectangular hyperbola because it represents the relationship better than a rectangular hyperbola at low photon flux density up to the point where the curve starts to bend (e.g. Prioul and Chartier, 1977; Goudriaan, 1978).

Leverenz (1979), Miranda (1982) and Griffiths (1983) have used the non-rectangular-hyperbola as it resulted in a better fit to the data in the light response curves of Sitka spruce needles.

In this study, the non-rectangular hyperbola was used as described by Thornley (1976) and used by Miranda (1982) and Griffiths (1983). The relationship between gross photosynthesis ( $F$ ) and photon flux density ( $Q$ ) as represented by the non-rectangular hyperbola is of the form:

$$\theta \cdot F^2 - (\alpha \cdot Q + F_m)F + \alpha \cdot Q \cdot F_m = 0 \quad 8.10$$

and

$$F = F_n + R_d \quad 8.11$$

$$F_m = F_{nm} + R_d \quad 8.12$$

where

$F$  is the gross photosynthesis ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )

$Q$  is the quantum flux density ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )

$F_m$  is the maximal (asymptotic) rate of photosynthesis at saturating quantum flux density ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )

$\theta$  is the convexity Coefficient

$\alpha$  is the initial slope of the light response curve ( $\mu\text{mol}/\mu\text{mol}$ )

$F_n$  is the rate of net photosynthesis ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )

$F_{nm}$  is maximal net photosynthesis rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )

$R_d$  is the rate of dark respiration ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )



The parameter  $\theta$  is the convexity coefficient which determines the non-rectangularity of the function, and enables a family of curves to be produced. For instance, Thornley (1976 p.94) showed curves with  $\theta$  ranging from zero to 1, where zero resulted in a rectangular hyperbola and 1 resulted in an extreme non-rectangular-hyperbola of two straight lines, the so-called Blackman response function.

The relationship between net photosynthesis and  $\text{CO}_2$  flux through the stomata to the intercellular spaces and then to the carboxylation sites in the mesophyll cells has been investigated (e.g. in conifers by Jarvis, 1980) and has been reviewed recently by Farquhar and Sharkey (1982). For a recent resumé, refer to Jones (1983 p.104-169) and papers by Jarvis (1981); Jarvis and Morrison (1981). The dependence of net  $\text{CO}_2$  uptake on stomatal conductance for water vapour indicates that as stomatal conductance approaches infinity, net photosynthesis is limited by the mesophyll component (refer to Jarvis 1981).

Thus, if over the operating range of the plant we assume a linear relationship between  $F_{nm}$  and  $C_i$  (Ludlow and Jarvis, 1971) with a slope  $g_m$

$$F_{nm} = g_m (C_i - \Gamma) \quad 8.13$$

where

$g_m$  is the mesophyll conductance ( $\text{mol m}^{-2} \text{s}^{-1}$ )

$C_i$  is the intercellular space  $\text{CO}_2$  concentration ( $\mu\text{mol mol}^{-1}$ )

$\Gamma$  is the  $\text{CO}_2$  compensation point ( $\mu\text{mol mol}^{-1}$ )

Note that this equation presumes physical diffusion of  $\text{CO}_2$  from intercellular space to the carboxylation sites at which the  $\text{CO}_2$  concentration is equal to the  $\text{CO}_2$  compensation point  $\Gamma$ .

The intercellular space  $\text{CO}_2$  concentration ( $C_i$ ) is influenced by stomatal opening. Stomata are known to be sensitive to  $\text{CO}_2$ , responding to  $\text{CO}_2$  concentration in the intercellular spaces. The stomata tend to open as intercellular space  $\text{CO}_2$  decreases (especially in  $C_4$  plants), though Jarvis (1980) showed that in conifers the stomata



are relatively insensitive to  $\text{CO}_2$ . This stomatal sensitivity to  $\text{CO}_2$  may be an important factor in the stomatal light response. Thus:

$$C_i = C_a - (F_n/g_s') \quad 8.14$$

where

$C_a$  is the ambient  $\text{CO}_2$  concentration ( $\mu\text{mol mol}^{-1}$ )  
 $g_s'$  is the stomatal conductance for  $\text{CO}_2$  ( $\text{mol m}^{-2}\text{s}^{-1}$ )

In a stirred porometer chamber, the boundary layer resistance  $r_a$  can be regarded as negligible; so that  $g_s'$  can be equated with stomatal conductance for water vapour. Thus:

$$\frac{g_s}{g_s'} = \frac{D(\text{H}_2\text{O})}{D(\text{CO}_2)} \quad 8.15$$

Where:

$D$  is the molecular diffusivity of water vapour or  $\text{CO}_2$   
 $g_s$  is stomatal conductance for water vapour.

This was measured by the LI-1600 in  $\text{cm s}^{-1}$ . To transform to  $\text{mol m}^{-2}\text{s}^{-1}$  the values were multiplied by 0.379 as given by Jones (1983) at  $30^\circ\text{C}$ . The value of the  $D(\text{H}_2\text{O})/D(\text{CO}_2)$  ratio has been discussed by Jarvis (1971) and is given as 1.605 being more or less independent of temperature and pressure. (The approximate conversion factor of 1.6 is often used where stomatal conductance to  $\text{H}_2\text{O}$  vapour and  $\text{CO}_2$  are not measured separately, assuming gas-phase paths for  $\text{CO}_2$  and water vapour are similar).

Substituting for  $C_i$  from equation 8.14 into equation 8.13 eliminates  $C_i$  and gives :



$$F_{nm} = [C_a - (F_n/g_s') - \Gamma]g_m \quad 8.16$$

Combining equations 8.10, 8.11 and 8.16 gives

$$\begin{aligned} & [\theta + (g_m/g_s')]F_n^2 + ([2\theta + (g_m/g_s')]R_d - [1 - (g_m/g_s')]\alpha.Q - (C_a - \Gamma)g_m)F_n \\ & + \alpha.Q[(C_a - \Gamma)g_m] + [R_d.\theta - \alpha.Q - ((C_a - \Gamma)g_m)]R_d = 0 \end{aligned} \quad 8.17$$

Equation 8.17 has a quadratic form  $ax^2 + bx + c = 0$  and can therefore be solved for  $F_n$  using the negative root of:

$$F_n = [-b \pm (b^2 - 4ac)^{0.5}] / 2a \quad 8.18$$

where

$$a = \theta + (g_m/g_s') \quad 8.19$$

$$\begin{aligned} b = & [2\theta + (g_m/g_s')]R_d - [1 + (g_m/g_s')]\alpha.Q - (C_a - \Gamma)g_m \\ & \alpha.Q - (C_a - \Gamma)g_m \end{aligned} \quad 8.20$$

$$c = \alpha.Q.g_m(C_a - \Gamma) + [R_d.\theta - \alpha.Q - (g_m(C_a - \Gamma))]R_d \quad 8.21$$

Equation 8.17 expresses net photosynthesis ( $F_n$ ) in terms of quantum flux ( $Q$ ), ambient  $CO_2$  concentration ( $C_a$ ), stomatal conductance for  $CO_2$  ( $g_s'$ ), mesophyll conductance for  $CO_2$  ( $g_m$ ), dark respiration ( $R_d$ ),  $CO_2$  compensation point ( $\Gamma$ ), convexity Coefficient ( $\theta$ ) and initial slope of the light response curve ( $\alpha$ ).

Of these variables  $Q$ ,  $C_a$  and  $g_s'$  can be derived from experimental values, other values may be estimated as parameters by solving the equation with observed values of  $F_n$  and  $g_s'$ . This procedure will be used in the following two chapters.

### 8.2.3 Stomatal module

At various times it was found necessary to fit a rectangular hyperbola to the observed relationship between stomatal conductance



and photon flux density. The stomata were not completely closed during the period when darkness was imposed on the leaves.

To correct for the values above zero in the dark, an additional 'dark opening' term was inserted:

$$g_s = \frac{g_{sm} \cdot Q \cdot \alpha_g}{(g_{sm} + \alpha_g \cdot Q)} + g_{sd} \quad 8.22$$

where:

$g_{sm}$  is the maximum stomatal conductance to  $CO_2$

$\alpha_g$  is the initial slope of the stomatal response curve  
(and it defines the shape of such curve)

$Q$  is the photon flux density.

$g_{sd}$  is the dark opening of the stomata.



## CHAPTER NINE

### **THE INFLUENCE OF PHOTON FLUX DENSITY DURING GROWTH ON THE SUBSEQUENT PHOTOSYNTHETIC RESPONSE TO LIGHT**

In Chapter 3 (section 3.2.2) a brief review on photosynthesis and respiration in response to shade was presented. The dependence of photosynthesis and respiration rates on photon flux density during growth was emphasized. It was noted also that plants occupying sunny habitats are generally capable of higher photosynthetic rates at high photon flux densities than plants restricted to shaded locations. This fact has been known for some time and is treated in detail by several authors in reviews on various aspects of photosynthetic response and adaptation to light (e.g. Björkman 1973, Boardman 1977, Osmond *et al* 1980, Björkman 1981). However, much more is known about temperate herbaceous plants and tree species than of tropical timber species in this respect; and consequently there is need for more research on various aspects of tropical tree physiology including photosynthetic response to light, both in the laboratory and field conditions.

In Chapter 7, it was demonstrated that there were significant changes in leaf properties, in particular chlorophyll content and specific leaf area as a result of growth at either low or high photon flux density (40 and 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  respectively). Transfer from HPD to LPD resulted in increased chlorophyll synthesis of the leaf whilst transfer from LPD to HPD resulted in chlorophyll decomposition of up to 50% in some species. There was a general similarity in species response as a result of growth at either LPD or HPD irrespective of whether they were thought of as light demanders or shade tolerators. However, the sedge, *Cyperus papyrus* responded differently from the tree species and did not tolerate shade at all.

Since leaves are the principal organs involved in photosynthesis, any changes in leaf properties are likely to have an influence on the photosynthetic performance of these species. The aim of the work described in this chapter is to analyse the influence of photon flux density during growth on the subsequent photosynthetic response of



*Terminalia superba*, *Terminalia ivorensis*, *Triplochiton scleroxylon*, *Khaya senegalensis* and the sedge *Cyperus papyrus*.

Assimilation rate has been expressed on both an area and weight basis to explore the influence of specific leaf area. The relationship between chlorophyll content and photosynthetic rate will be discussed.

### 9.1 Materials and methods

The same plants and light regimes as reported in Chapter 7 were used. However, only those plants that had remained at HPD or LPD throughout the 5 weeks growth period were analysed, ignoring those that had experienced a transfer between the light regimes. Five plants of each of the tree species from each of the light regimes (LPD and HPD) and *C. papyrus* seedlings grown at HPD were used to assess the photosynthetic gas exchange characteristics; the tree plants being chosen at random after a further two weeks of growth in the Fisons growth cabinet (see Section 7.2.2). From each of these plants, a fully expanded leaf was put in the porometer chamber ( $2 \text{ cm}^2$  for tree species,  $1 \text{ cm}^2$  for *C. papyrus*),  $\text{CO}_2$  and water vapour exchanges were assessed at 0, 1%, 5%, 12%, 25%, 50% and 100% of the incident photon flux. This gave a range of conditions from dark to nearly  $1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$  (the classes were chosen to allow adequate sampling over the photon flux range limiting to photosynthesis, yet also allowing photon flux densities that were saturating).

All experiments were carried out on attached leaves in the Fisons cabinets. For *C. papyrus*, only plants at HPD were analysed as those at LPD had not survived to this point.

The methods for measurement of  $\text{CO}_2$  and water vapour exchanges have been described and presented in Chapter 8.

### 9.2 Data analysis

To assess the statistical significance of the treatment effects, analysis of variance was applied using the GENSTAT package. Following



this, both rectangular and non-rectangular hyperbolae were fitted to the data using the parameter optimisation program PAR within the BMDP package. It was found that the non-rectangular hyperbola was in most cases a marginally better fit, and so only this one will be reported henceforth.

### 9.3 Results

#### 9.3.1 Stomatal conductance to water vapour

Stomatal conductance was strongly influenced by both the prevailing photon flux density and that to which the plants had been exposed during growth (see Appendix Table A1 for analysis of variance). However, the mean conductances of the four tree species were not significantly different from each other, but there were significant interactions between species and light.

Stomatal conductance was influenced by growth conditions (HPD or LPD), being higher when plants had been grown at HPD (Fig. 9.1a). *C. papyrus* displayed very high conductance values (Fig. 9.1b) at HPD and the stomata were more wide open even when dark conditions were imposed than in the tree species in bright light during the period of measurements.

The parameter values obtained when the non-rectangular hyperbola was fitted to the conductance data are given in Table 9.2 (for tree species). The algorithm to calculate the conductance for each species, based on this set of parameter values, will be referred to as the stomata module (see also Section 8.2.3).

#### 9.3.2 Effect of photon flux density on photosynthetic rate expressed on an area basis

Analysis of variance (Appendix Table A2) showed that the prevailing photon flux density during measurements, growth conditions (HPD and LPD), species and the interaction of these three factors had significant effects ( $P < 0.001$ ) on  $\text{CO}_2$  assimilation rates.



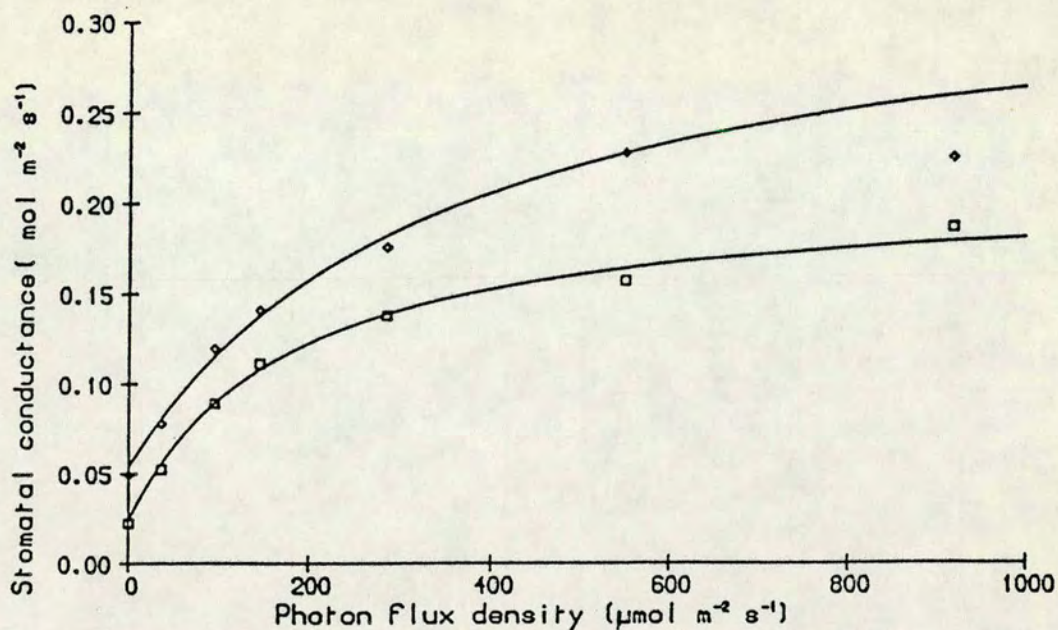


FIGURE 9.1a : The effect of growth at LPD ( $\square$ ) and HPD ( $\diamond$ ) on stomatal conductance to water vapour. Data for the tree species have been pooled as explained in text. Parameters used in curve fitting are presented in Table 9.2.

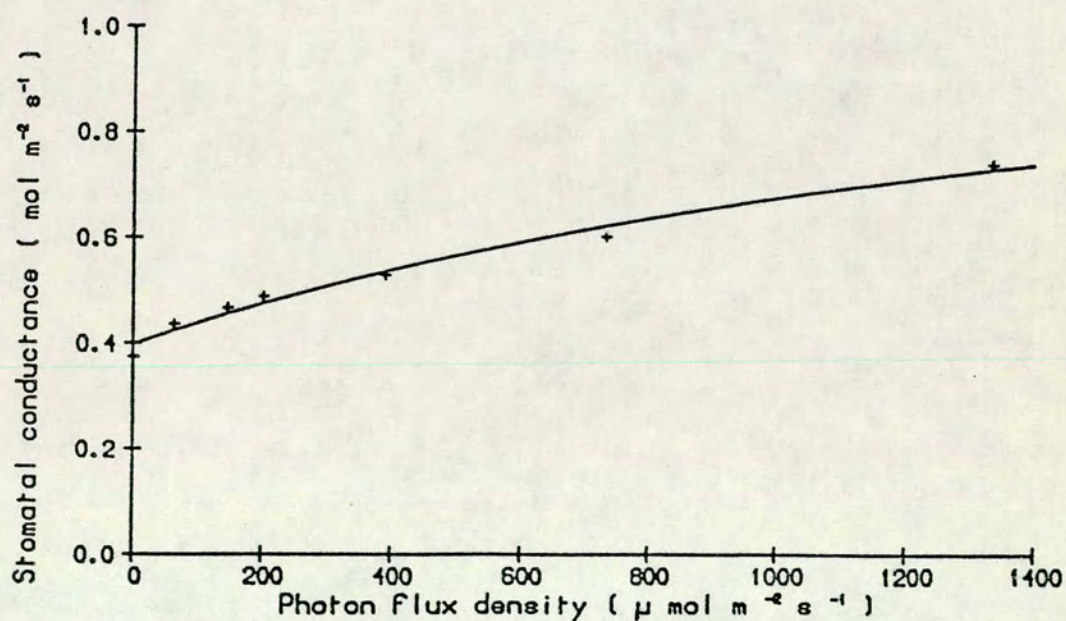


FIGURE 9.1b : The effect of growth at HPD on stomatal conductance to water vapour in *Cyperus papyrus* seedlings.



TABLE 9.1

SPECIES	Growth Conditions	$\theta$	a	$g_m$	$R_d$	Rss	Mse	n
<i>T. superba</i>	LPD	0.993 (0.027)	0.0388 (0.0072)	0.0198 (0.0017)	0.287 (0.299)	19.32	0.62	32
	HPD	0.935 (0.064)	0.0342 (0.0045)	0.0359 (0.0023)	0.344 (0.241)	13.94	0.45	32
	LPD	0.941 (0.107)	0.0313 (0.0088)	0.015 (0.0015)	0.36 (0.259)	11.86	0.38	32
<i>K. senegalensis</i>	HPD	0.00099	0.1065 (0.0413)	0.0242 (0.0028)	1.59 (0.533)	47.83	1.49	32
	LPD	0.930 (0.073)	0.0441 (0.0085)	0.0174 (0.0011)	0.438 (0.19)	5.97	0.19	32
<i>Triplochiton scleroxylon</i>	HPD	0.0099	0.0958 (0.0177)	0.0515 (0.003)	1.27 (0.408)	30.16	0.94	32
	LPD	0.944 (0.107)	0.0176 (0.0044)	0.0158 (0.0016)	0.436 (0.226)	9.99	0.32	32
<i>T. ivorensis</i>	HPD	0.716 (0.389)	0.0388 (0.0138)	0.0399 (0.006)	0.992 (0.534)	47.99	1.55	32
	HPD	0.591 (0.538)	0.0281 (0.0056)	0.0926 (0.031)	2.23 (0.506)	34.05	1.42	25
<i>Cyperus papyrus</i>								

TABLE 9.1: The values of parameters and their associated errors from the photosynthetic model as evaluated using a non-rectangular hyperbola fitted to the data of each species when grown at either LPD or HPD. Curves drawn from these parameters and those in Table 9.6 can be seen in Fig. 9.4. (For *Cyperus papyrus* see Fig. 9.4e). Parameter symbols and abbreviations as given in the table :

LPD and HPD are 40 and 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  respectively;  $\theta$  is the convexity coefficient; a is the initial slope of the light response curve (the apparent quantum efficiency  $\mu\text{mol CO}_2/\mu\text{mol quanta}$ );  $g_m$  is the mesophyll conductance to  $\text{CO}_2$  ( $\text{mol m}^{-2} \text{s}^{-1}$ ), Rss is the residual sum of squares; Mse is the mean square error; () encloses the asymptotic standard deviation at n degrees of freedom.



The stomata module referred to above were then used in the photosynthesis model (Table 9.1) to cater for the influence of stomata on photosynthesis. Finally the model was run to generate calculated rates of photosynthesis in the form of response curves, and the original observations placed on the graphs to enable visual judgement of goodness of fit.

When data for the four tree species are pooled in order to investigate the effects of growth conditions on photosynthesis, the estimated photosynthetic response reached a maximum value under HPD (Fig. 9.2). The result of incorporating the stomata module (Table 9.2) into the photosynthesis model (Table 9.3), and the mean values of observed photosynthesis rate showed that :

- (i) Plants grown at HPD displayed maximum photosynthesis rates which were about twice those grown at LPD.
- (ii) Plants raised at HPD also displayed higher (more negative) rates of dark respiration.

After analysis of species response by combining the data of growth at HPD and LPD, and then fitting the photosynthesis model (Table 9.4) and stomata module (Table 9.5) to the data, one clear difference emerges: of the tree species, *Khaya senegalensis* displayed lower rates of photosynthesis than the other species (Fig. 9.3).

Further analysis was carried out on individual species to investigate the effects of growth at LPD and HPD on photosynthetic response. The stomata module (Table 9.6) and the photosynthesis model (Table 9.1) were fitted to the data. The resulting light response curves of  $\text{CO}_2$  uptake showed that:

- (i) *Khaya senegalensis* (Fig. 9.4b) did not display a very much higher rate of photosynthesis when grown at HPD than at LPD, whilst all other species did.
- (ii) *Cyperus papyrus* (Fig. 9.4e) displayed higher rates of



TABLE 9.2:

Growth Conditions	$g_s$ (light)	$a_g$	$g_s$ (dark)	Rss	Mse	n
LPD	0.185 (0.0099)	0.00106 (0.000018)	0.0238 (0.0059)	0.116	0.000806	137
HPD	0.284 (0.0209)	0.000825 (0.000136)	0.0536 (0.0069)	0.189	0.000134	137

Table 9.2: Parameter values obtained by fitting the stomata module to the conductance data. In this case, the data for different tree species have been pooled to investigate the general effect of light regime during growth. The curves drawn from these parameters and those in Table 9.3 can be seen in Fig. 9.1a.

Parameter symbols and abbreviations given in the table :

LPD and HPD are 40 and 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  respectively,  
 $g_s$  (light) is the asymptotic stomatal conductance to water vapour in the light ( $\text{mol m}^{-2} \text{s}^{-1}$ ),  
 $a_g$  is the initial slope of the stomatal-light response curve ( $\mu\text{mol H}_2\text{O}/\mu\text{mol quanta}$ ),  
 $g_s$  (dark) is the dark opening of the stomata. It may be regarded as the residual conductance to water vapour in the dark. This opening is probably due to stomata remaining open, possibly a component of the cuticular water loss.  
Rss is the mean square error  
n are degrees of freedom  
() encloses the asymptotic standard deviations at n degrees of freedom.



TABLE 9.3:

Growth Conditions	$\theta$	$a$	$g_m$	$R_d$	$R_{ss}$	$Mse$	$n$
LPD	0.927 (0.069)	0.0394 (0.0068)	0.0171 (0.001)	0.473 (0.164)	80.78	0.59	136
HPD	0.0099	0.0698 (0.0011)	0.0417 (0.0022)	1.109 (0.306)	302.48	2.21	137

Table 9.3 : Photosynthesis model: final parameters values found as described in the text, applied to the data from LPD and HPD shows predicted response for growth at LPD and HPD. In this case the data for the four different tree species were pooled to investigate the general effect of light regime during growth. Curves drawn from these parameters can be seen in Fig. 9.2.

Parameter symbols and abbreviations given in the table :

LPD and HPD are 40 and 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  respectively;

$\theta$  is the convexity coefficient

$a$  is the initial slope of the light response curve (the apparent quantum efficiency  $\mu\text{mol CO}_2/\mu\text{mol quanta}$ )

$g_m$  is the mesophyll conductance to  $\text{CO}_2$  ( $\text{mol m}^{-2} \text{s}^{-1}$ )

$R_{ss}$  is the residual sum of squares

$Mse$  is the mean square error

$n$  are degrees of freedom

( ) enclose the asymptotic standard deviation



TABLE 9.4

Species	Growth Conditions	$\theta$	$a$	$g_m$	Rd	Rss	Mse	n
<i>T. superba</i>	LPD and HPD	0.936 (0.107)	0.0393 (0.0081)	0.0284 (0.0024)	0.421 (0.299)	83.26	1.26	66
<i>K. senegalensis</i>	LDP and HPD	0.0099	0.0854 (0.0262)	0.0209 (0.0016)	1.029 (0.308)	66.80	0.99	67
<i>Triplochiton scleroxylon</i>	LPD and HPD	0.0099	0.0938 (0.027)	0.0352 (0.003)	1.012 (0.487)	171.28	2.56	67
<i>T. ivorensis</i>	LPD and HPD	0.714 (0.446)	0.0362 (0.0162)	0.0295 (0.0046)	0.977 (0.482)	164.01	2.48	66

Table 9.4: Photosynthesis model: parameter values obtained as described in the text. In this case data for each species at LPD and HPD were pooled and fitted to a non-rectangular hyperbola to investigate species differences in photosynthetic rates. Together with data presented in Table 9.5, curves drawn from these parameters can be seen in Fig. 9.3.

Parameter symbols and abbreviations in the table :

LPD and HPD are 40 and 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  respectively;  $\theta$  is the convexity coefficient;  $a$  is the initial slope of the light response curve (the apparent quantum efficiency  $\mu\text{mol CO}_2/\mu\text{mol Quanta}$ );  $g_m$  is the mesophyll conductance to  $\text{CO}_2$  ( $\text{mol m}^{-2} \text{s}^{-1}$ );  $R_{ss}$  is the residual sum of squares;  $n$  are degrees of freedom;  $( )^m$  enclose the asymptotic standard deviation.



TABLE 9.5

SPECIES	Growth Conditions	$g_s$ (light)	$a_g$	$g_s$ (dark)	Rss	Mse	n
<i>T. superba</i>	LPD and HPD	0.239	0.00078	0.0401	0.11	1.65	67
<i>K. senegalensis</i>	LPD and HPD	0.164	0.00158	0.0474	0.13	1.95	67
<i>Triplochiton scleroxylon</i>	LPD and HPD	0.243	0.00132	0.0261	0.037	0.56	67
<i>T. ivorensis</i>	LPD and HPD	0.304	0.00061	0.0315	0.13	2.0	67

Table 9.5 shows the predicted stomatal response of each species. Data for growth at LPD and HPD were pooled. Curves drawn from the parameters in conjunction with those in Table 9.4 can be seen in Fig. 9.3

Parameter symbols and abbreviations in the table:

LPD and HPD are 40 and 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  respectively;  $g_s$  (light) is the stomatal conductance to water vapour in light ( $\text{mol m}^{-2} \text{s}^{-1}$ ) (this is the asymptotic value);  $a_g$  is the initial slope of the stomatal-light response curve ( $\mu\text{mol H}_2\text{O}/\mu\text{mol Quanta}$ );  $g_s$  (dark) is dark opening of the stomata. It may be regarded as the residual conductance to water vapour in the dark. This opening is probably due to the stomata remaining open, probably a component of cuticular water loss; Rss is the residual sum of squares; n are degrees of freedom;

Note that asymptotic standard deviations are missing. The values were very small in magnitude.



TABLE 9.6

## SPECIES

	Growth Condition	$g_s$ (light)	$a_g$	$g_s$ (dark)	Rss	Mse	n
<i>T. superba</i>	LPD	0.165 (0.0091)	0.00106 (0.000191)	0.0257 (0.0055)	0.62	1.94	32
	HDP	0.365 (0.0791)	0.000664 (0.000212)	0.0525 (0.0133)	4.94	15.4	32
	LDP	0.184 (0.0264)	0.00148 (0.000703)	0.0160 (0.0174)	5.49	1.72	32
	HPD	0.147 (0.0165)	0.00180 (0.000715)	0.0763 (0.0123)	2.69	8.42	32
<i>Triplochiton scleroxylon</i>	LPD	0.199 (0.012)	0.00150 (0.000298)	0.0282 (0.0079)	1.15	3.58	32
	HPD	0.293 (0.019)	0.00117 (0.000117)	0.0449 (0.0083)	1.50	4.70	32
	LPD	0.236 (0.0222)	0.0005 (0.000094)	0.0193 (0.0061)	8.22	2.57	32
	HPD	0.380 (0.0586)	0.0007 (0.000193)	0.0438 (0.0137)	4.11	12.8	32
<i>Cyperus papyrus</i>	HPD	0.773 (0.269)	0.00043 (0.000112)	0.3985 (0.0152)	4.15	16.6	25

Table 9.6 : The results of fitting the stomatal module to stomatal conductance data. These estimated parameters were used in conjunction with the photosynthesis model (Table 9.1). Curves drawn from these parameters can be seen in Fig. 9.4 (for tree species) and 9.4e (for *Cyperus papyrus*). Parameter symbols and abbreviations as given in the table: LPD and HPD are 40 and 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  respectively;  $g_s$  (light) is the stomatal conductance for water vapour in light ( $\text{mol m}^{-2} \text{s}^{-1}$ );  $a_g$  is the initial slope of the stomata-light response curve ( $\mu\text{mol H}_2\text{O}/\mu\text{mol quanta}$ );  $g_s$  (dark) is dark opening of the stomata; Rss is the residual sum of squares; n are degrees of freedom; ( ) enclose the asymptotic standard deviation.



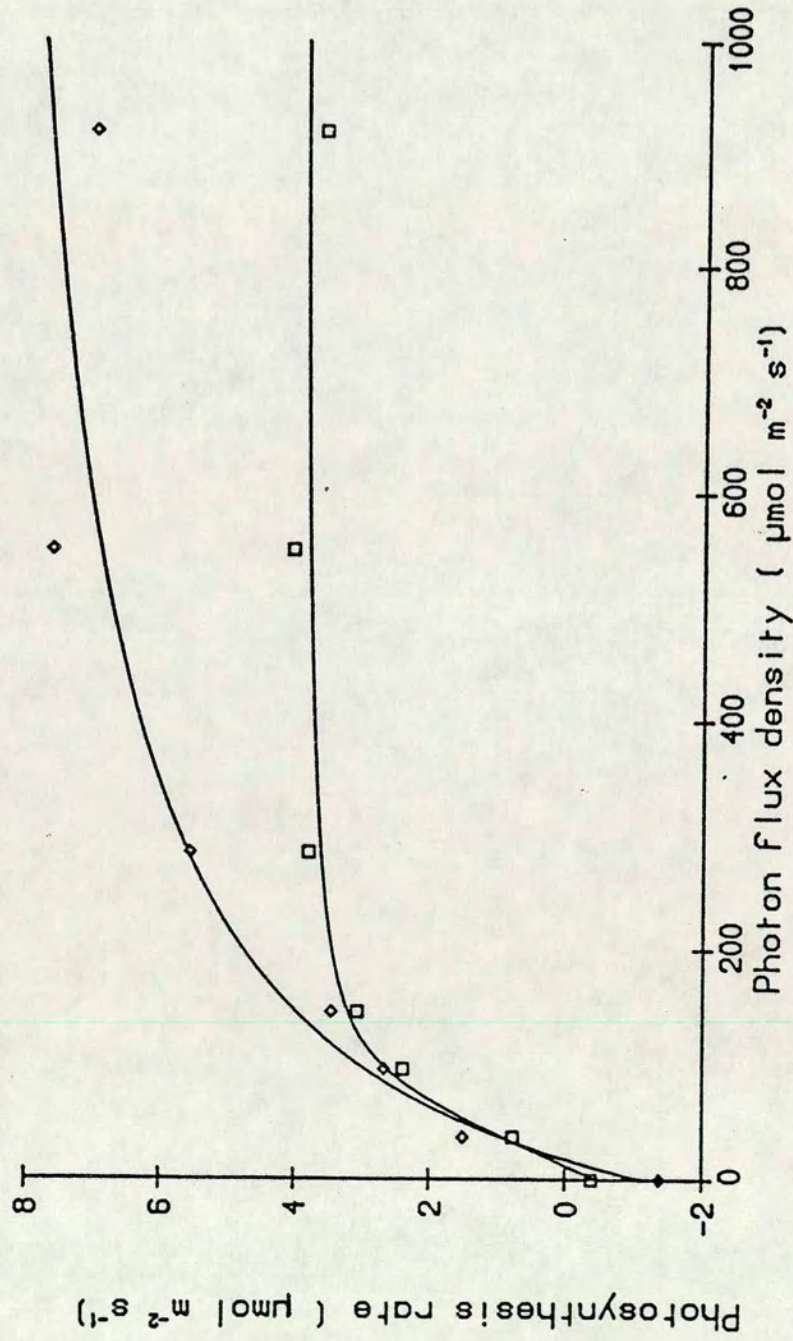


FIGURE 9.2 : Photosynthetic response as a result of growth at LPD (□) and HPD (◇). Data for the four tree species have been pooled as explained in the text to investigate the general effect of growth conditions. Parameters used in curve fitting are presented in Tables 9.2 and 9.3.



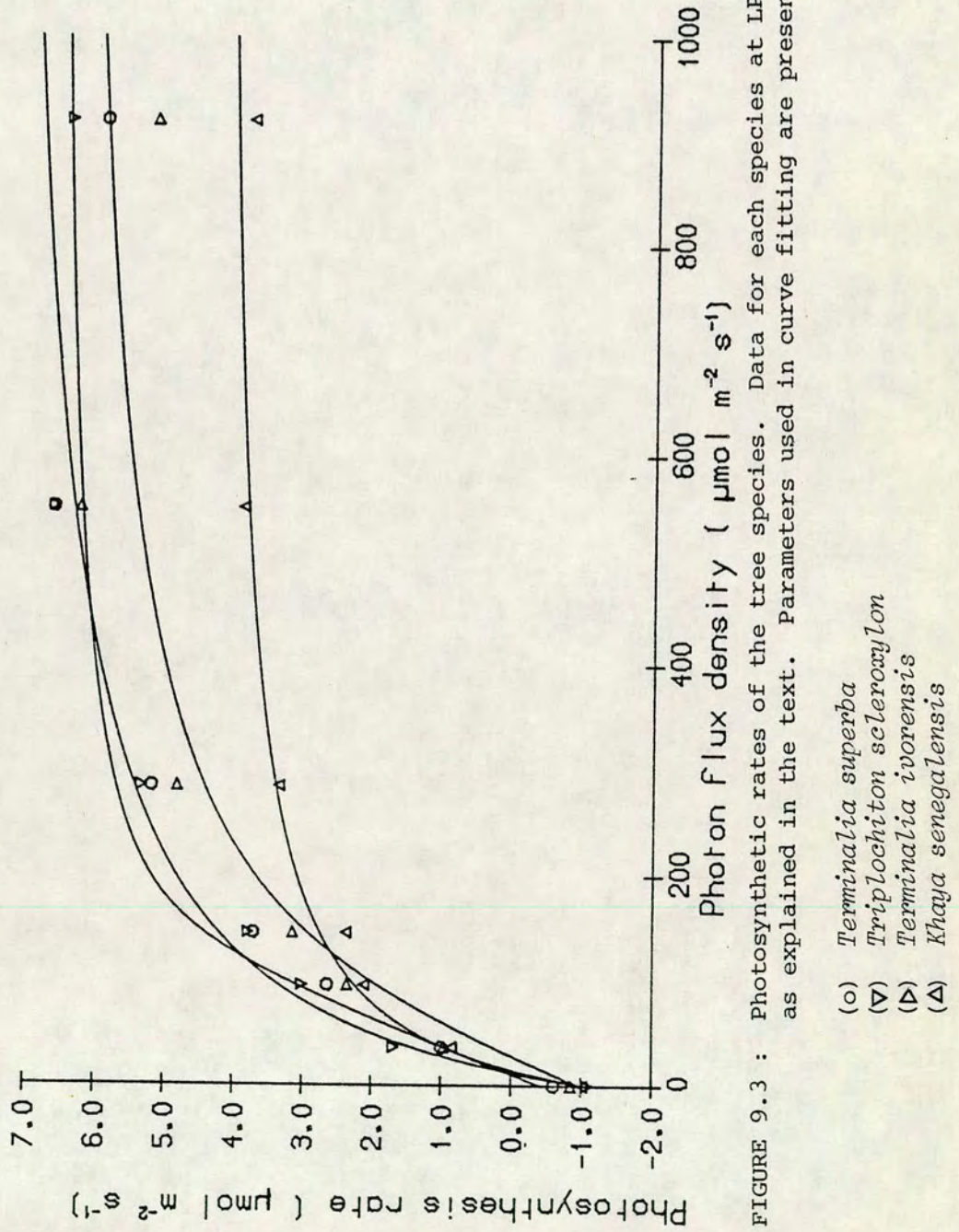


FIGURE 9.3 : Photosynthetic rates of the tree species. Data for each species at LPD and HPD were pooled as explained in the text. Parameters used in curve fitting are presented in Tables 9.4 and 9.5.



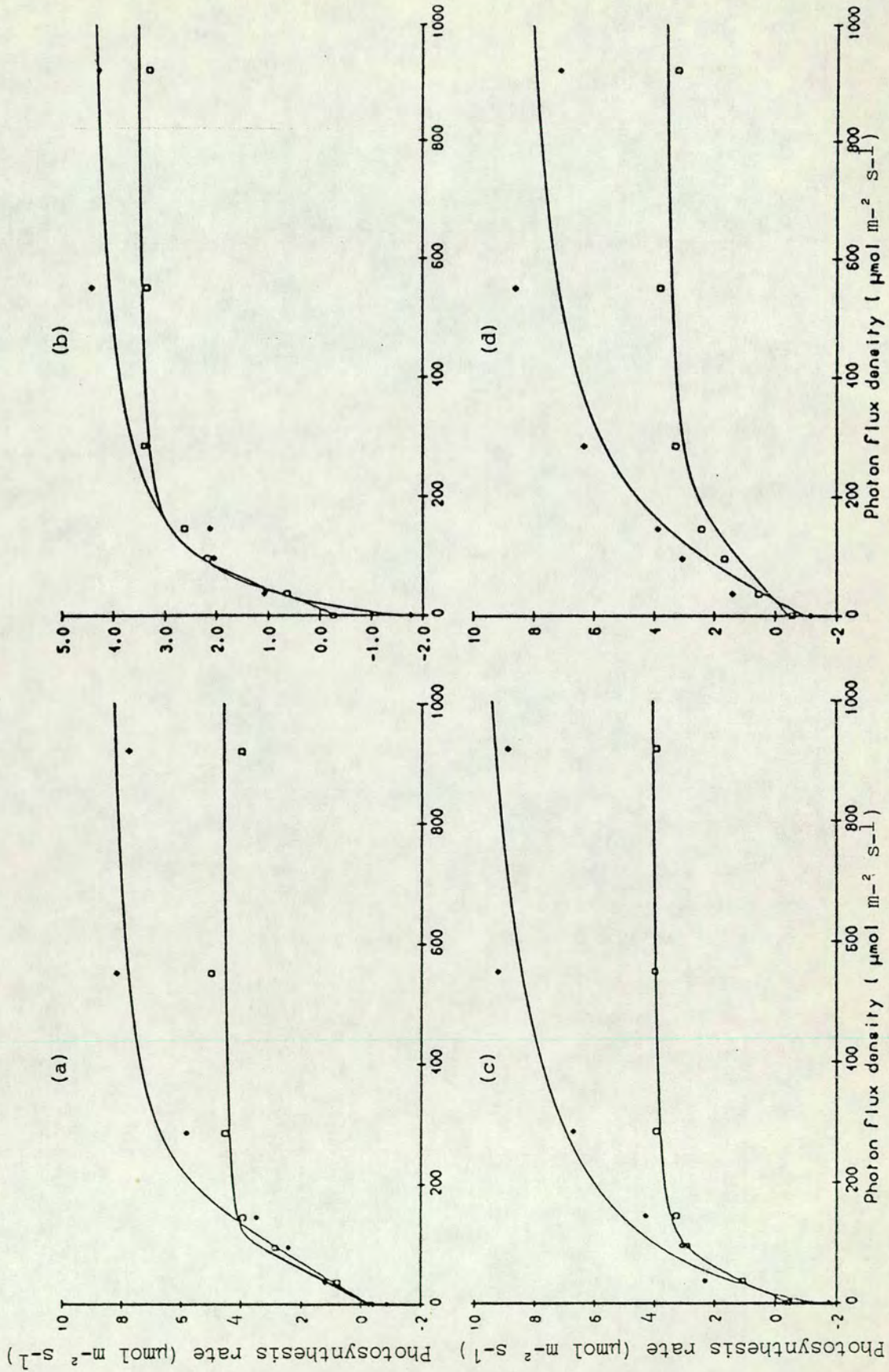


FIGURE 9.4a - d : The effect of growth at LPD (□) and HPD (●) on photosynthetic response of (a) *Terminalia superba* (b) *Khaya senegalensis* (c) *Triplochiton scleroxylon* (d) *Terminalia ivorensis*. Parameters used in curve fitting are presented in Tables 9.1 and 9.6. Note the change in scale of the y axis in (b).



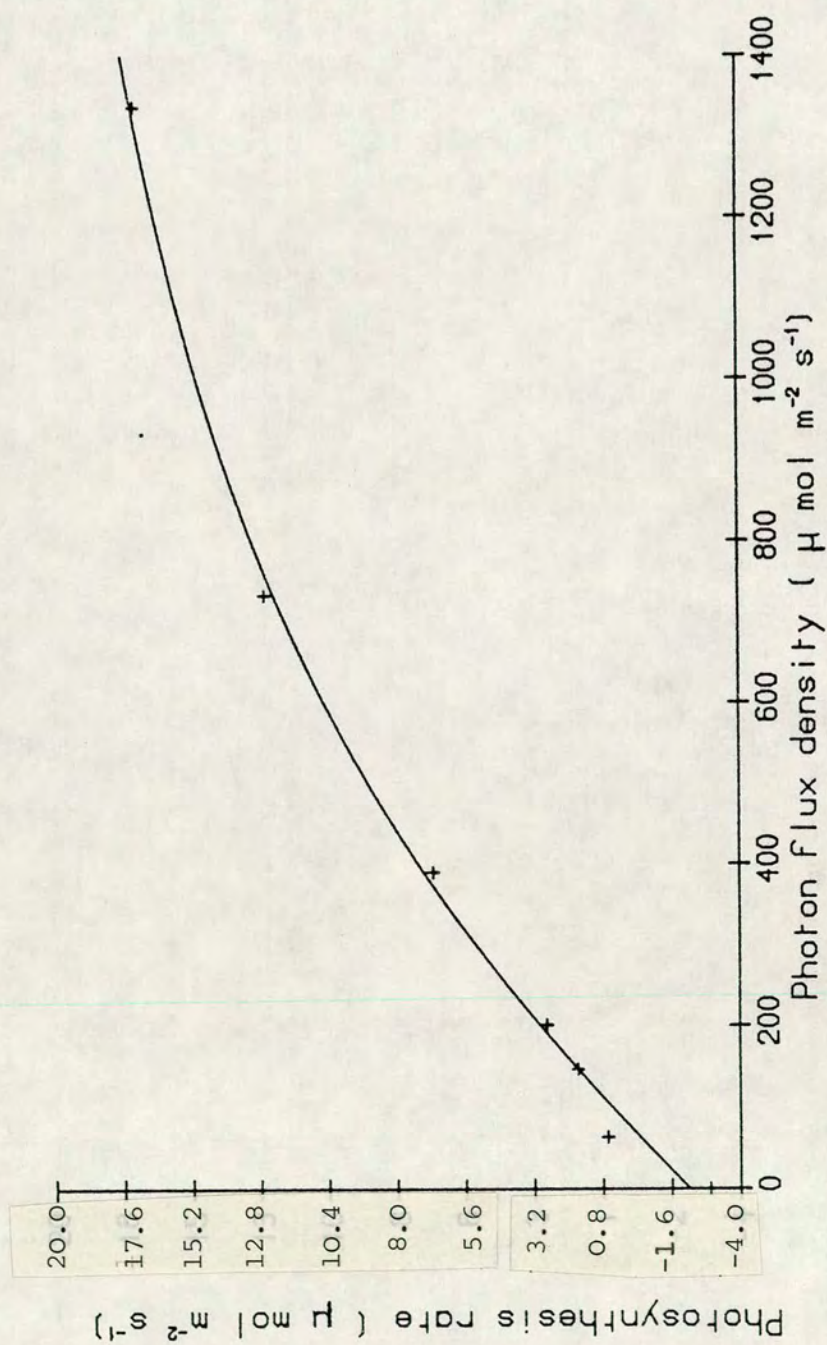


FIGURE 9.4e : The effect of growth at HPD on the photosynthetic response of *Cyperus papyrus* .  
Parameters used in curve fitting are presented in Tables 9.1 and 9.6.



photosynthesis than the tree species. It also displayed higher (more negative) rates of dark respiration and was not light saturated at photon flux densities that were saturating for tree species.

### 9.3.3 Effect of photon flux density on the photosynthesis rate (re-expressed on a dry weight basis)

When re-expressed on a dry weight basis, a quite different picture emerged among the tree species. It was the plants which had been grown at LPD which displayed the highest assimilation rates, irrespective of current illumination (Appendix Table A3, Fig. 9.5). There is a clear difference between species as a result of growth at LPD (Fig. 9.6a) and HPD (Fig. 9.6b): *Khaya senegalensis* and *Terminalia ivorensis* displaying lower rates of photosynthesis throughout. For *Cyperus papyrus*, growth at HPD (Fig. 9.6c) still resulted in higher photosynthetic and respiration rates than the tree species.

## 9.4 Discussion

### 9.4.1 Problems of data analysis

Some of the problems associated with data analysis by non-linear regression methods are well presented by Ross (1981): considerations include=

- (i) Some models are more appropriate than others. Choice between rival models should be done cautiously, bearing in mind the error distribution and magnitudes. According to Ross (1981), fitting models is not simply a matter of smoothing scattered data to make them look more respectable; on the contrary, it is a method of estimating particular quantities from the data. It is also a method of testing whether the model fits the data either statistically in terms of variance ratio (F) test or graphically in terms of general pattern of data points relative to the fitted curves; to compare different models which may be related or unrelated and to obtain more precisely estimates of common parameters. It is generally advantageous if the measured quantities have physical or biological meaning.



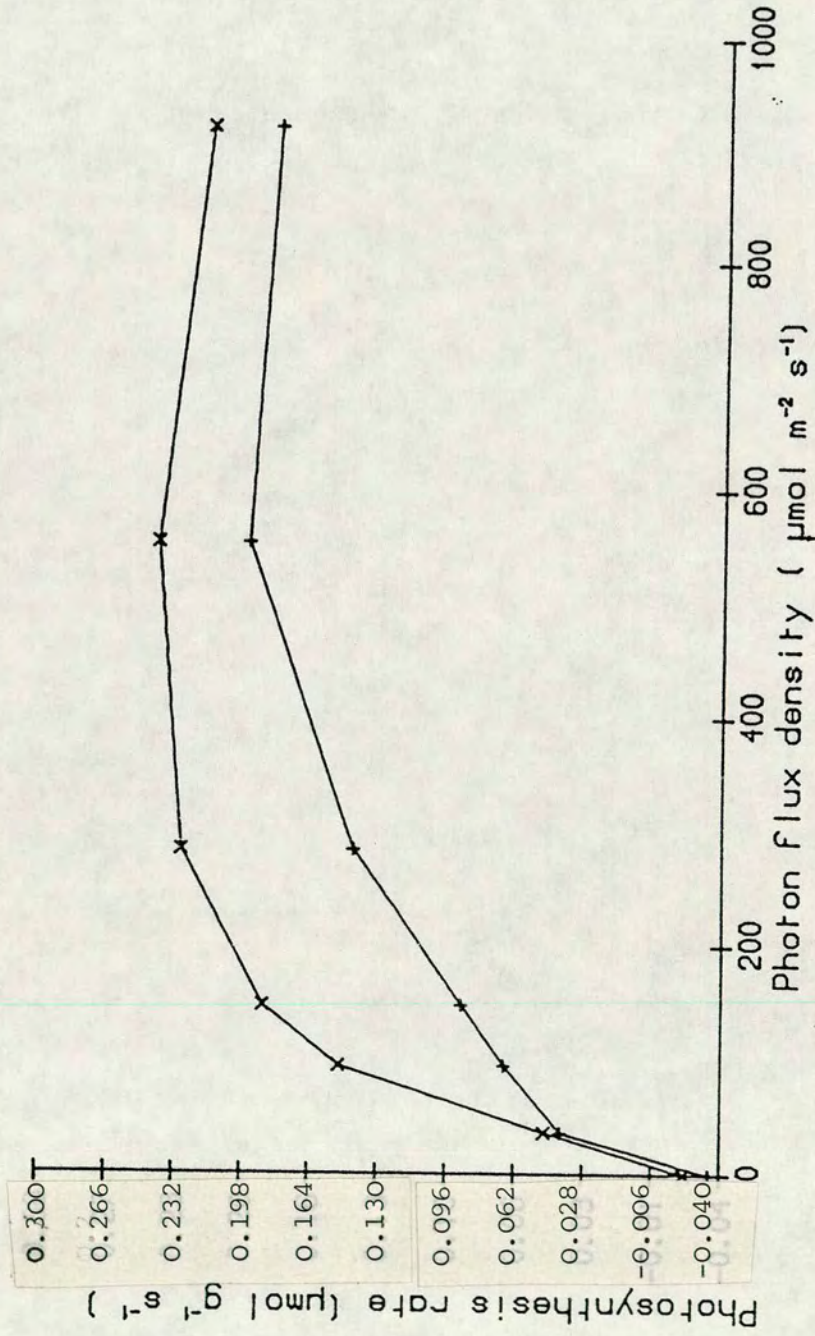


FIGURE 9.5: The effect of growth at LPD (x) and HPD (+) on the photosynthetic response of the tree species (expressed on a dry weight basis). Mean values joined by a straight line.



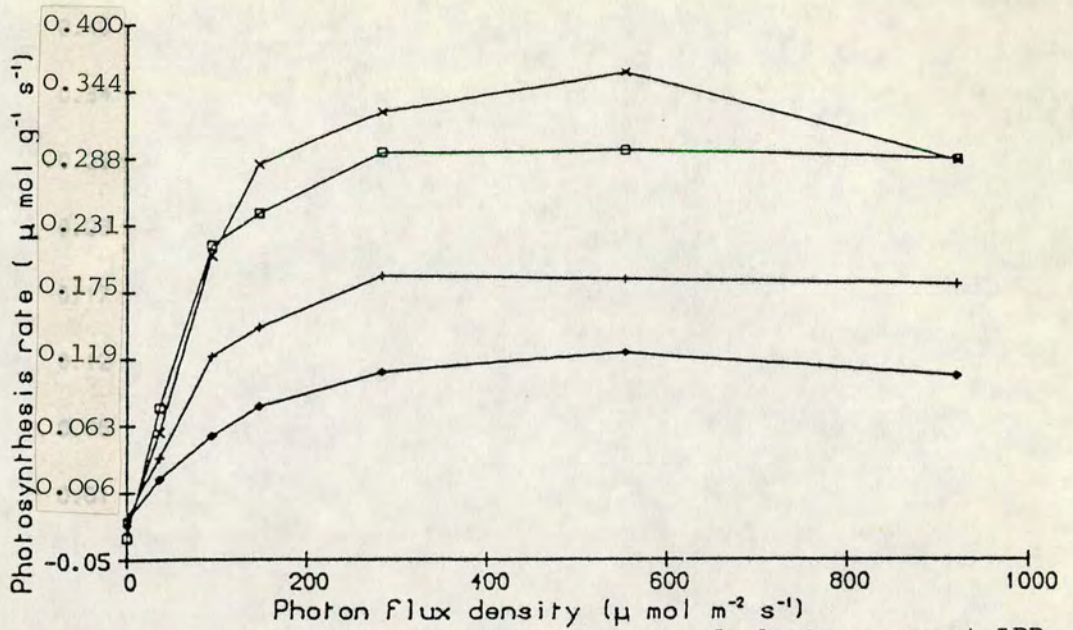


FIGURE 9.6a : The photosynthetic response of plants grown at LPD (expressed on a dry weight basis).

- (x) *Terminalia superba*      (□) *Triplochiton scleroxylon*  
 (+) *Khaya senegalensis*      (◆) *Terminalia ivorensis*

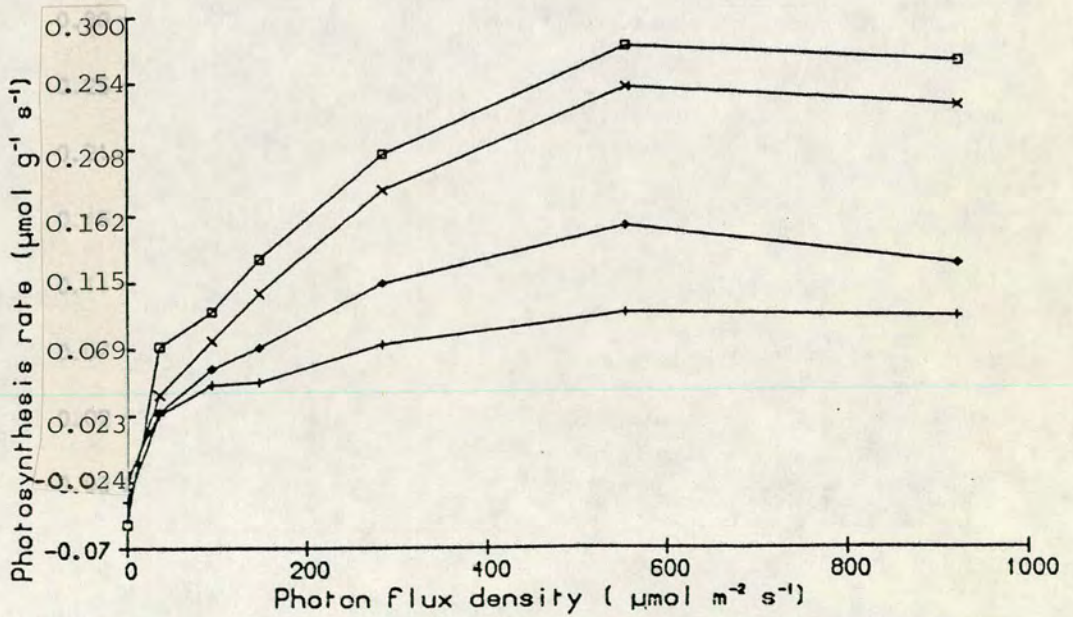


FIGURE 9.6b : Photosynthetic response of plants grown at HPD (expressed on a dry weight basis).

- (□) *Triplochiton scleroxylon*  
 (x) *Terminalia superba*  
 (◆) *Terminalia ivorensis*  
 (+) *Khaya senegalensis*



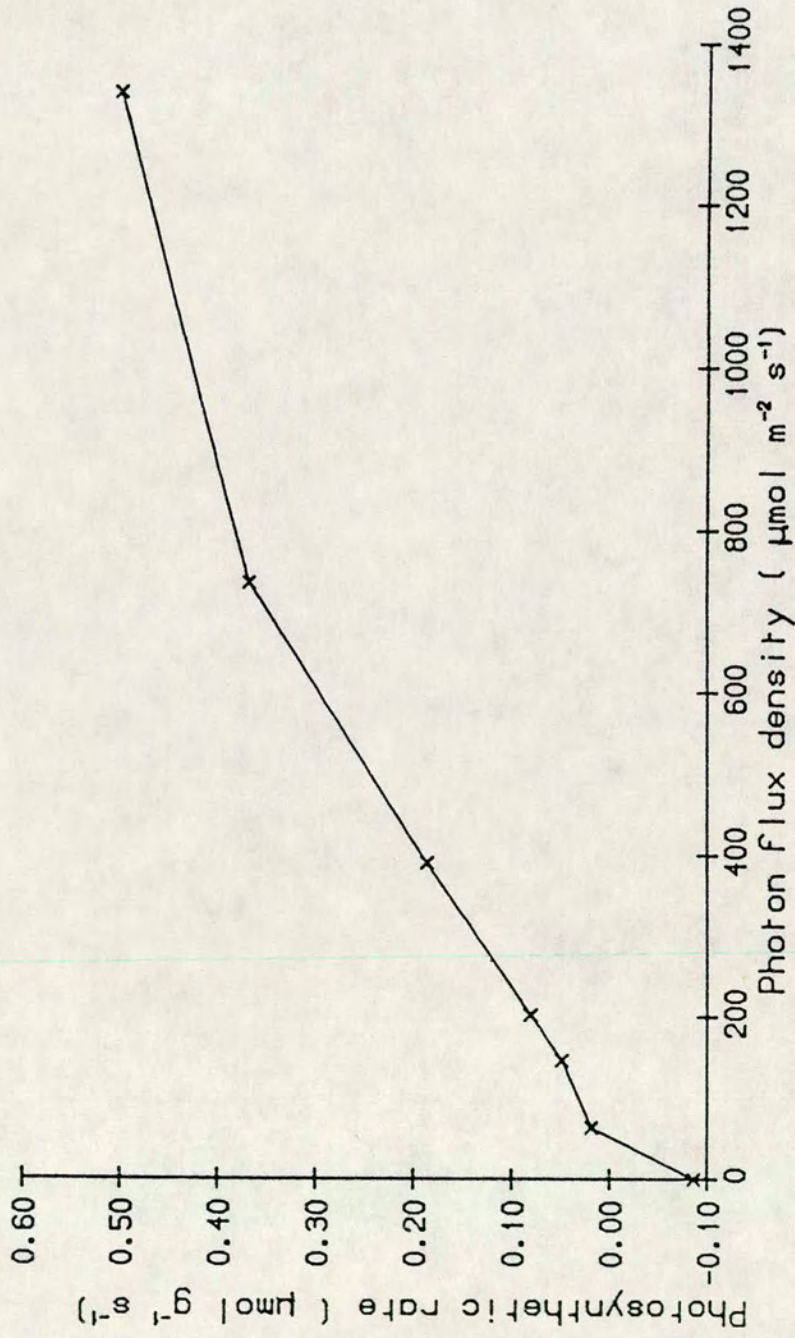


FIGURE 9.6c : The effect of growth at HPD on photosynthetic response (expressed on a dry weight basis) of *Cyperus papirus* seedlings.



(ii) It is extremely difficult to judge from inspection of the fitted parameters, standard errors and correlations, whether parameters are significantly different especially if the data are observed over different ranges on the x axis.

In the present experiments, these problems were encountered and dealt with as described. Analysis of variance (Appendix Tables A1, A2 and A3) shows that the rates of photosynthesis indeed depend on the light regime during growth. Objection may be raised against the use of analysis of variance in such cases as the variance may well increase with the increase in the mean, over the range of photon flux densities (see Snedecor and Cochran, 1967). However, when the data were reanalysed, after logarithmic transformation to overcome this problem, the essential conclusions were not affected. It was noted that after logarithmic transformation the level of significance was sometimes changed, but that the list of treatments declared significant at  $P < 0.05$  did not change (e.g. Appendix Table A4).

Following this, the choice of fitting the non-rectangular hyperbola (Table 9.1) as opposed to the rectangular hyperbola was dictated by the fact that the former resulted in slightly lower residual sum of squares and mean square errors. It also yields a useful extra parameter, theta, that enables the curve to be fitted accurately to the data near the point of light saturation. This is best illustrated by inspection of Figure 9.4a : here the transition from light-limited to light-saturated photosynthesis is markedly dependent on the light regime during growth. The difference between the two treatments cannot be represented unless the non-rectangular hyperbola, with its additional parameter, theta, is used.

Finally, the fitted parameters do have recognisable biological or biophysical meaning. Conductances and respiration rates derived as model parameters may be directly compared with those in the literature. Alpha, the initial slope of the light response curve is nearly synonymous with the quantum efficiency of photosynthesis (not exactly synonymous because the input data describing the photon flux represents incident rather than absorbed photons). Theta is a more



difficult quantity to interpret, but may represent an index of the degree of mutual shading between chloroplasts within a unit area of leaf, itself dependent on leaf thickness as well as structural organisation at tissues and cellular levels.

#### 9.4.2 Relationship between chlorophyll content and photosynthetic rates

In Chapter 7, leaf properties as a result of growth at LPD and HPD were investigated in terms of chlorophyll content and specific leaf area. In this chapter the results of photosynthetic characteristics of leaves developed at LPD and at HPD are presented. One of the main objectives of this study is to explore if there is an obvious relationship between chlorophyll content and capacity for photosynthesis or between chlorophyll content and quantum efficiency at this level of investigation.

It is unlikely that photosynthetic rate at saturation will ever depend on chlorophyll content in normal leaves. Šesták (1966) discussed the limitation for finding a linear relationship between chlorophyll content and photosynthetic activity. It is well known that when chlorophyll depletion becomes clearly visible (e.g. with nutritional deficiencies and pathological situations, or before leaf abscission); the leaves are incapable of utilizing high photon flux densities sufficiently. Besides, the photosynthetic rate is controlled by so many variables, both environmental and biochemical. Whereas photosynthesis involves gas exchange in physical and biochemical states, chlorophyll participation concerns the trapping and utilization of the absorbed quanta which is a photochemical as well as a biochemical process. It is also well established that chlorophyll synthesis and degradation go on simultaneously in the leaf chloroplasts. The leaf environment (both external and internal) and genetic factors influence the overall photosynthetic performance of leaves. Thus it is difficult to establish a strong direct relationship between chlorophyll content and light saturated photosynthesis; perhaps at a finer level of investigations, such correlations do exist, but this is outside the scope of this thesis.



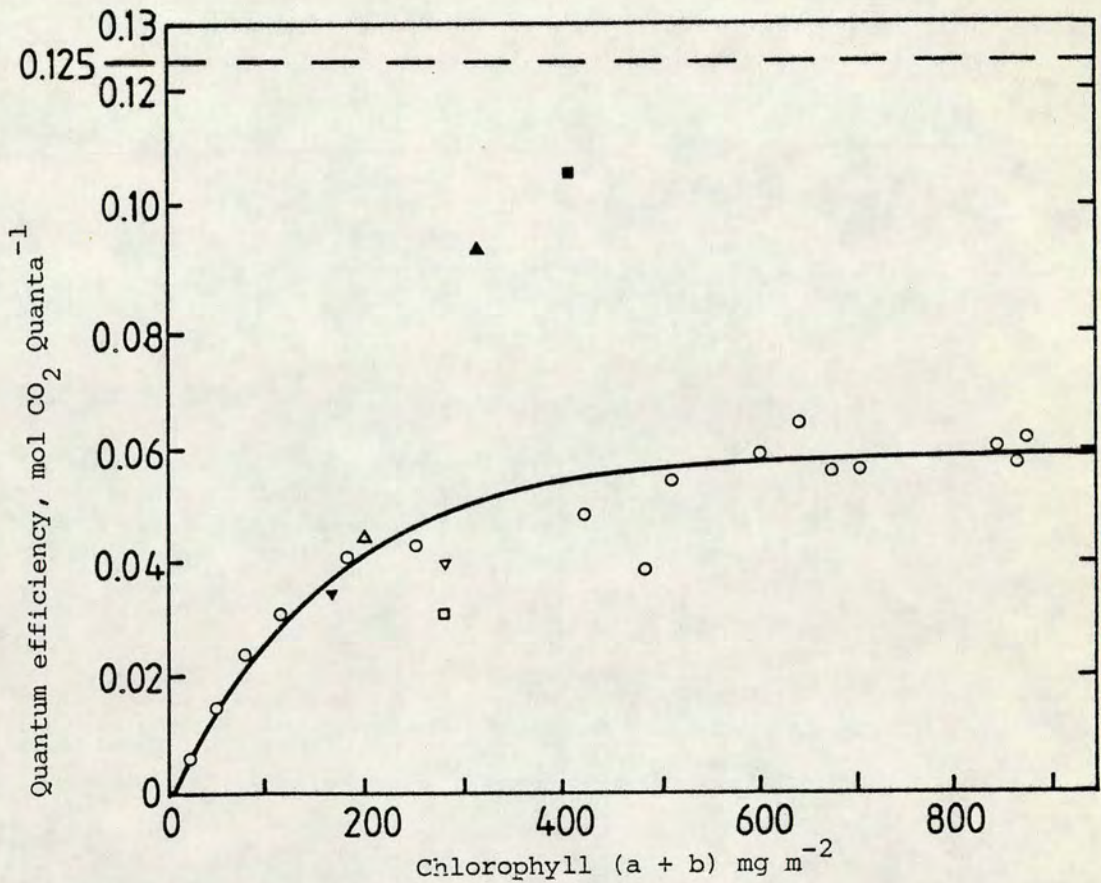


FIGURE 9.7: Relationship between chlorophyll content and apparent quantum efficiency. Data for chlorophyll content of some of the tree species in the experiments described in Chapter 7 has been compared to Gabrielsen's (1948) data (○) as discussed in the text. Chlorophyll content for the tree species after four weeks growth at either LPD or HPD in the Fison's cabinet is presented (Table 7.2), and the apparent quantum efficiency at LPD and HPD is shown (Table 9.1).

The species involved are :

*Terminalia superba* at LPD (▽) and HPD (▼)  
*Triplochiton scleroxylon* LPD (Δ) and HPD (▲)  
*Khaya senegalensis* LPD (□) and HPD (■)

---- is the theoretical maximum quantum efficiency assuming 8 moles of quanta fix one mole of  $\text{CO}_2$ . Usually 8-10 moles of quanta are needed for fixing 1 mole of  $\text{CO}_2$  (e.g. Walker, 1979, p.15).



In the review by Björkman (1981), recent studies suggest poor correlation between chlorophyll content and net photosynthesis. He cites examples of 49 different sun and shade species grown under different light regimes. The general trend in the differences between light saturated photosynthetic rates in sun and shade leaves of the same species were not related to the estimated chlorophyll content. The evidence also suggests that the capacity of component steps of photosynthesis which determine the absorption and trapping of light quanta probably has little or no impact on light saturated photosynthetic rate.

It is however likely that quantum efficiency will be related to chlorophyll content. The data in Chapter 7 of chlorophyll content and the apparent quantum efficiency estimated from the data in Chapter 9 were compared to that of Gabrielsen (1948) as shown in Figure 9.7. There appears to be only a weak relationship, which is perhaps to be expected as the capture of photons by chlorophyll must depend not only on the amount of chlorophyll but also its organisation. Also, the relationship is not linear. For values above  $400 \text{ mg m}^{-2}$  the leaves appear not to increase their quantum efficiency. It seems that these leaves have 'reserves' of chlorophyll, perhaps a safeguard against photodestruction (see Gabrielsen's data of 1948).

In their review of photosynthetic characteristics of wet tropical plants, Mooney *et al.*, (1984) implicated nitrogen content as the strong determinant of leaf photosynthetic capacity rather than chlorophyll content. They reported that leaves of rainforest dominants have a relatively high nitrogen content, which also varies greatly with leaf age. They were surprised to find low light saturated photosynthetic rates ( $3.4 - 8.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) in the Mexican pipers in spite of their high nitrogen content. They attributed this to be probably due to investment in nitrogen-based defensive compounds such as alkaloids in this species rather than the photosynthetic machinery.

Thus, species variation in net photosynthesis and apparent quantum efficiency cannot be accounted for by variations in chlorophyll content.



Nevertheless, within each species there appears, in the present study, to be a weak relationship between the chlorophyll content and the apparent quantum efficiency: the light regime which causes the highest chlorophyll content also causes the highest apparent quantum efficiency. However, the data are not sufficiently extensive to enable conclusions to be drawn as to whether light demanders and shade tolerators are different in this respect.

#### 9.4.3 Photosynthetic rates at light saturation

In general, shade leaves and shade plants show lower rates of photosynthesis than sun species at light saturation. As was shown (Figs. 9.3, 9.4 and 9.6b) the shade tolerant *Khaya senegalensis* displayed the lower rates of photosynthesis at saturation than the light demanding tree species when grown at either LPD or HPD, and its light saturated photosynthetic rates at HPD were similar in magnitude to those of the other species mentioned above when grown at LPD.

Compared to the shade tolerant *Khaya senegalensis*, the light demanding tree species in this experiment showed more capability in dealing with extreme variations in the light environment, adjusting their photosynthetic capacities to cope with the prevailing light regime. They behaved rather like shade plants when grown in dim light, and switched from low to high rates of photosynthesis when grown at HPD.

Similar observations were made by Bazzaz and Carlson (1982) in 14 early, middle and late successional plants grown outdoors in full sunlight and under the shade of a dense Mulberry canopy. In the present study, *Khaya senegalensis* displayed low rates of photosynthesis and showed practically no ability to adjust to higher rates when grown at HPD. Perhaps *Khaya senegalensis* only responds to R/FR ratio under reduced PAR during growth (see Chapter 10).

Evidence from other workers on sun and shade species e.g. Björkman (1981) suggests that obligate shade plants have an intrinsically low potential for photosynthetic light acclimation (environmentally induced adaptation) and an inherent low ability to increase their capacity for effective utilization of high quantum flux densities for



photosynthesis. In this respect, *Khaya senegalensis* behaved like a true obligate shade plant when grown at HPD. Moreover, the photosynthetic behaviour of the tree species in this experiment can be compared with the results of Björkman and Holmgren (1963) on *Solidago virgaurea*. When cloned individuals of sun and shade ecotypes were grown at low and high photon flux densities, growth of the shade clone was retarded under HPD and there was no increased capacity for light saturated photosynthesis. In addition, high quantum flux densities during growth caused a reduction in the quantum yield at rate-limiting quantum flux densities of the shade clones; which Björkman (1968) attributed to a low capacity of such plants to increase their level of ribulose - 1, 5-bisphosphate carboxylase.

Other evidence as presented in the recent review on this topic by Björkman (1981) suggests that the low potential of obligate shade plants to increase their light saturated photosynthetic capacity in response to increased photon flux density during growth may be a result of photoinhibition of the reaction centres due to excessive excitation energy (see also Chapter 7). Tolerance of high photon flux densities may be related to the ability to dissipate this excessive energy via photosynthesis as observed in the response of the light demanders. For shade plants, Björkman (1981) suggests that other alternative mechanisms for safe dissipation of, or protection against, the potentially harmful effects of excessive excitation energy may also play an important role, e.g. mechanisms for long term repair of components that are inactivated or destroyed in photoinhibition may be important as well. However, the high susceptibility to photoinhibition of shade plants may constitute an even greater selective disadvantage, and this is likely to increase when other stresses are present.

For example, in ecological considerations of adaptation to sun and shade habitats, apart from the light regime, sun and shade habitats differ; sunny habitats tend to be drier than densely shaded locations, and water stress may also lead to photoinhibition.

The species difference in this experiment has ecological implications. Fast growing light demanding tree species may make full



use of large gaps in the canopy through high photosynthetic capacities in response to increased photon flux density whilst slow growing shade tolerant species may be shaded by such plants in the gap because of their inherent low potential to increase their photosynthetic capacity. However, species like *Khaya senegalensis* may benefit from sunflecks through other adaptive mechanisms such as high apparent quantum efficiency and <sup>Low</sup>respiration rates as discussed in the proceeding section.

#### 9.4.4 Dark respiration rates

Table 9.7 shows dark respiration rates on both an area and weight basis as a result of growth at LPD and HPD. The final column is the ratio of respiration at LPD to that at HPD, when expressed on a weight basis.

Species	Growth Conditions	Compensation point $\mu\text{mol m}^{-2}\text{s}^{-1}$	Dark respiration $\mu\text{mol CO}_2\text{ m}^{-2}\text{s}^{-1}$	Dark respiration $\mu\text{mol CO}_2\text{ g}^{-1}\text{s}^{-1}$	$\frac{R_{\text{LPD}}}{R_{\text{HPD}}}$
<i>Terminalia</i>	HPD	16	- 0.34	-0.0268	0.929
<i>superba</i>	LPD	8	- 0.29	-0.0249	
<i>Triplochiton</i>	HPD	15	- 1.00	-0.0534	0.595
<i>scleroxylon</i>	LPD	10	- 0.44	-0.0318	
<i>Terminalia</i>	HPD	25	- 1.30	-0.0207	0.864
<i>ivorensis</i>	LPD	25	- 0.44	-0.0179	
<i>Khaya</i>	HPD	20	- 1.60	-0.0378	0.386
<i>senegalensis</i>	LPD	10	- 0.36	-0.0146	
<i>Cyperus</i>	HPD	70	- 2.23	-0.0724	-
<i>papyrus</i>					



As shown (Fig. 9.4, Table 9.7) all the tree species displayed lower dark respiration rates when grown at LPD than at HPD; because of this, extremely low photon flux densities were sufficient to maintain the carbon balance.

Light compensation point is a useful parameter in an ecological sense and depends on the apparent quantum efficiency and respiration rate. The light compensation points for the tree species ranged from 8- 25  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in both LPD and HPD conditions. However, in *Terminalia ivorensis* the light compensation point was 25  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for both LPD and HPD grown plants. In other species, growth at LPD resulted in lower light compensation points. Similar magnitudes have been reported by Langenheim *et al* (1984) for three emergent tree seedlings of Amazonian rainforest canopies and two Araucarian conifer seedlings of the tropical Australian rainforest, grown at 6 % (shade) and 100 % full sunlight (sun) in glasshouses. *Cyperus papyrus* (Table 9.7, Fig. 9.4e) had a much higher light compensation (70  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) at HPD than the tree species, as expected for a  $\text{C}_4$  plant.

A high rate of dark respiration at HPD may be a consequence of a rapid growth rate, with the need for high rates of mobilization of assimilates from the leaves to the regions of rapid utilization. Quite apart from the role of respiration in transport, the maintenance of organisation at a chloroplast level is presumably associated with the expenditure of energy. For this reason, plants with high rates of photosynthesis and high quantum efficiency may necessarily have a high rate of dark respiration. Plants in dim light require low respiratory rates if they are to make efficient use of the available light through a conservative use of assimilates. Such low respiratory losses are necessarily coupled with slow rates of metabolism under such low photon flux densities.

In Table 9.7, we have calculated the ratio of dark respiration under LPD to HPD ( $R_{\text{LPD}}/R_{\text{HPD}}$ ), using the data expressed on a weight basis. This ratio is lowest in the shade-tolerant *Khaya senegalensis* and highest in the light demanding *Terminalia* spp; it is intermediate in *Triplochiton scleroxylon* which is not an aggressive light-demander. This



ratio seems to indicate the ranking of shade-tolerant and light-demanding species. Thus, the lower the value the more shade-tolerant the species; and the higher the value, the more light-demanding the species. It is highly suggestive, but it may not be conclusive. It is noteworthy that this relationship does not hold when the ratio is calculated on an area basis. The weight basis is perhaps a more fundamental measure in respiration studies since respiration is not functionally related to leaf area (as photosynthesis is), but dependent on enzymes which may notionally at least be considered in concentrations in terms of weight per volume of leaf or weight per weight of leaf.

Other studies on tropical tree species such as Langenheim *et al* (1984) on seedlings of Caesalpinoids: *Hymenaea courbaril*, *H. parvifolia* and *Copaifera venezuelana*, emergent trees of Amazonian rainforest canopies and two Araucaria conifers: *Agathis microstachya* and *A. robusta* in tropical Australian rainforests grown in glasshouses at 6 % and 100 % full sunlight conditions; respiration rates for mature leaves measured at 22 and 27 °C, were in the range of 0.03 - 0.41  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ . The values were higher for the Araucarias and full sunlight seedlings than for shade (6 % of full sunlight) and Caesalpinoids of the Amazon rainforest canopies. Moreover, Pearcy and Calkin (1983) on *Claoxylon sandwicense* an understorey sapling of Hawaii, and Ladipo *et al.*, (1984) on six clones of *Triplochiton scleroxylon* reported higher values of respiration rates than those of Langenheim *et al.*, (1984) but similar values (0.32 - 0.77  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) to those reported in this experiment for LPD conditions, yet lower than those at HPD for *Triplochiton scleroxylon*, *Terminalia ivorensis* and *Khaya senegalensis*.

The efficient use of available light by shade leaves and shaded plants has been associated with low dark respiration. Björkman (1981) pointed out that such plants should also have lower contents of certain chloroplast components needed to maximize efficiency in dim light. For example, Goodchild *et al.*, (1972) found that leaves of shade plants have considerably less soluble protein content (15 - 25%) than the sun leaves with a similar chlorophyll content, and this diminished with decreasing photon flux density for a given sun plant. This was attributable to a



much lower content of RuBP carboxylase in shade plants and presumably also the content of other enzymes involved in photosynthetic carbon metabolism is reduced in shade plants.

The results of this experiment showed that shaded plants displayed lower rates of dark respiration irrespective of whether the plants were light demanders or shade tolerators. This characteristic is important in the maintenance of a positive carbon balance of shaded leaves as is possible in a crown of a single tree species. Also, forest trees show a high degree of adaptation to the prevailing light regime. Nevertheless, the shade tolerant *Khaya senegalensis* displayed characteristics of shade leaves by operating at low photosynthetic rates at HPD and LPD.

#### 9.4.5 Leaf structure and photosynthesis of sun and shade leaves

Throughout this study, it has been re-affirmed that specific leaf area is indeed strongly influenced by the light regime during growth. Growth at HPD resulted in thicker leaves with a low specific leaf area whilst growth at LPD resulted in thinner leaves with a high specific leaf area. These thicker leaves always displayed a higher mesophyll conductance.

The influence of SLA on chlorophyll content (Chapter 7) showed that more chlorophyll was synthesized by leaves grown at LPD when this was expressed on a leaf dry weight basis. In this chapter, the influence of SLA was clearly evident. The photosynthetic performance at LPD or HPD on a dry weight basis was in a reverse ranking compared to that expressed on an area basis (compare Fig. 9.2 with 9.5); on a dry weight basis it was the plants that were grown at LPD which displayed higher rates of photosynthesis than those at HPD. Moreover, the re-ranking was pronounced in species performance (Fig. 9.6a) and it was *Terminalia ivorensis* which displayed the lowest photosynthetic rates. Nevertheless, at HPD, both on an area and leaf dry weight basis (compare Figs. 9.3 and 9.6b) *Khaya senegalensis* displayed the lowest photosynthetic rates.



Anatomical examinations by other workers on typical  $C_3$  plants (see review by Björkman, 1981) shows that sun leaves are characterized by the presence of well developed palisade parenchyma with a high proportion of long columnar cells, whilst in shade leaves the mesophyll cells tend to be round or highly irregular in shape; and the total number of cells across a leaf section is often smaller in shade leaves than sun leaves. This suggests a close packing of cells with fewer and smaller air spaces in sun leaves that results in a low specific leaf area and a corresponding high specific leaf weight.

There are two major considerations pertaining to the relationship between leaf anatomy and photosynthetic capacity. One concerns the amount of photosynthetic apparatus per unit leaf area whilst the other concerns the internal area of exposed mesophyll cells ( $A_{mes}$ ) per unit leaf area ( $A$ ).

The changes in leaf thickness during growth at high photon flux densities have been associated with increased mesophyll volume to unit leaf area (ratio  $(V_{mes}/A)$  and mesophyll area to unit leaf area ratio ( $A_{mes}/A$ ) and these contribute to the increase in leaf thickness and specific leaf weight. These changes occur in both sun and shade species at HPD. In sun species, the photosynthetic capacity on an area basis tends to increase with increasing  $V_{mes}/A$  and  $A_{mes}/A$  ratio over a wide range of light levels, whereas in obligate shade species, increases in these ratios often are not accompanied by increases in photosynthetic rates. Then, if increases in these rates reflect increases in potentially rate-limiting catalysts (such as RUBP carboxylase and electron carriers) per unit leaf area, light-saturated photosynthetic capacity would be expected to increase as well; and both the  $CO_2$ -limited and the  $CO_2$ -saturated photosynthetic rate may be affected by such changes at the chloroplast level.

Björkman (1981) argues that it seems likely that in plants which have a high potential for acclimation to different light regimes, the amount of these components per mesophyll area or volume remains more or less constant over a wide range of such light regimes. The alternative mode of response would be an increase in the concentration



of these compounds in the chloroplasts or cell as the photon flux density during growth is increased. However, it is probable that there is an intrinsic upper limit to which such increases in concentration may occur; there is evidence for example, that RUBP carboxylase concentration in the chloroplast approaches the solubility limit of this protein. It is also possible that the spatial distribution of the  $\text{CO}_2$  acceptor sites on the enzyme may be important for efficient capture of  $\text{CO}_2$ , especially at limiting  $\text{CO}_2$  pressures, and that certain relationships between the number of carboxylation sites, chloroplast area and cell wall area are necessary for efficient utilization of low intercellular  $\text{CO}_2$  concentrations. This is outside the scope of this thesis, but such increases in the amounts of the above mentioned components of the photosynthetic system and the area of exposed mesophyll cell walls may enable such plants to capture more efficiently the available PAR.

There is little evidence, however, that differences in light saturated photosynthesis rates between different species are attributable to differences in  $A_{\text{mes}}/A_{\text{ratio}}$ , or that diffusive transfer of  $\text{CO}_2$  between the intercellular air spaces and the chloroplasts imposes a major limitation to photosynthesis in  $\text{C}_3$  plants grown in native habitats or simulated conditions as prevailing in their native habitats. Although cell packing was not investigated in this study, the mesophyll values estimated from the model (Table 9.1) are very useful and this will be discussed in Chapter 11.



## CHAPTER TEN

**THE INFLUENCE OF RED/FAR-RED RATIO (R/FR) DURING GROWTH AT LOW PAR ON THE SUBSEQUENT GAS EXCHANGE CHARACTERISTICS OF LEAVES**

In Chapter 6, growth analysis of *Khaya senegalensis* and *Terminalia ivorensis* seedlings grown under similar photon flux densities with different R/FR ratios was presented. It was shown that the main effect of a reduction in R/FR ratio was to increase specific leaf area (SLA) in *Terminalia ivorensis* with a corresponding increase in relative growth rate (RGR). Such increases were not observed in *Khaya senegalensis*: RGR and SLA were slightly lower under low R/FR than under high R/FR. It was also shown that at high R/FR, *Terminalia ivorensis* responded by an increase in net assimilation rate (NAR) whilst *Khaya senegalensis* did not differ in NAR with or without a variation in R/FR ratio.

These results showed that the two species responded differently under similar conditions, and identified a specific response to R/FR which is independent of any response to photosynthetically active radiation.

In this chapter, an attempt to characterize the influence of the R/FR ratio during growth on the subsequent gas exchange characteristics is presented.

**10.1 Materials and methods**

Seedlings of the same source as in Chapter 6 (Section 6.2.4) were used. These seedlings remained in the glasshouse for 12 weeks before they were transferred to the Fisons growth cabinet on 16/10/83.

Twenty seedlings of *Khaya senegalensis* and *Terminalia ivorensis* were grown in the Fisons cabinet at  $125 \mu\text{mol m}^{-2} \text{s}^{-1}$  PAR (see Section 6.2). 10 seedlings of each species were grown at high R/FR (1.7) and the other ten seedlings at low R/FR (0.28). The R/FR ratio was varied by use of cinemoid filters as already described (Section 6.2.2).



At the time of transfer to the Fisons growth cabinet, there were very young leaves on the terminal shoot of *Terminalia ivorensis*. After five weeks of growth in the Fisons cabinet, gas exchange characteristics and SLA were examined. Five plants of each species from low and high R/FR ratio regimes were randomly selected for CO<sub>2</sub> and water-vapour exchanges. Of each of these plants, a fully expanded attached leaf was investigated as described in Chapter 8.

After CO<sub>2</sub> and water-vapour exchanges were measured, the same leaves were cut off and their leaf areas recorded in the normal way, after which they were oven dried for 48 hours at 90 °C in order to calculate the SLA.

#### 10.1.2 Data analysis

The same methods as reported in Chapter 9 (Section 9.2) were adopted and used in the curve fitting procedure. Assimilation rates were expressed on both an area and weight basis in order to explore the influence of specific leaf area.



## 10.2 Results

Under low R/FR ratio the SLA was higher than under high R/FR (Table 10.1).

PAR = 125 $\mu\text{mol m}^{-2}\text{s}^{-1}$	<i>Khaya senegalensis</i>		<i>Terminalia ivorensis</i>	
	Low R/FR (0.28)	High R/FR (1.7)	Low R/FR (0.28)	High R/FR (1.7)
Number of replicate				
leaves	5	5	5	5
Mean SLA ( $\text{cm}^2 \text{mg}^{-1}$ )	0.39	0.29	0.67	0.49
Standard error	0.03	0.02	0.16	0.17

Table 10.1. The mean specific leaf area of the two species after 5 weeks in the Fisons cabinet. Included are some of the leaves that had already developed on the terminal shoots from the glasshouse before the treatment began. About three out of the five leaves analysed had been influenced by glasshouse conditions in both species.

### 10.2.1 The influence of R/FR ratio during growth at low PAR on stomatal conductance

Analysis of variance (Appendix Table A5) showed no significant differences in stomatal conductance to water vapour between species or R/FR ratio during growth. There was a small interaction effect between species and R/FR ratio during growth, but it was barely significant ( $P < 0.05$ ). Stomata were open in the dark and the opening increased with increasing photon flux density imposed during gas exchange measurements.



Table 10.2a:

Species	Growth Conditions	$\theta$	a	$g_m$	Rd	Rss	Mse	n
Both <i>Khaya</i> and <i>Terminalia</i>	Low R/FR	0.0567 (0.0756)	0.0975 (0.0357)	0.0306 (0.0028)	0.623 (0.243)	40.62	0.61	66
	High R/FR	0.0099	0.0816 (0.014)	0.0234 (0.0013)	0.850 (0.205)	29.82	0.44	67

Table 10.2a: Photosynthesis model: Estimated parameters and errors when the non-rectangular hyperbola was fitted to the pooled data of *Khaya senegalensis* and *Terminalia ivorensis* to investigate the general effect of R/FR ratio on photosynthesis. Curves drawn from these parameters and those in Table 10.2b can be seen in Fig. 10.1.

Parameter symbols and abbreviations as given in the table:

Low and High R/FR are 0.28 and 1.70 respectively;  $\theta$  is the convexity Coefficient;

a is the initial slope of the light response curve ( $\mu\text{mol CO}_2/\mu\text{mol quanta}$ );

$g_m$  is the mesophyll conductance to  $\text{CO}_2$  ( $\text{mol m}^{-2} \text{s}^{-1}$ ); Rss is the residual sum of squares;

Mse is the mean square error; n are degrees of freedom; () enclose the asymptotic standard deviation at n degrees of freedom.



TABLE 10.2b:

SPECIES	Growth Conditions	$g_s$ (light)	$a_g$	$g_s$ (dark)	Rss	Mse	n
Both <i>Khaya</i> and <i>Terminalia</i>	Low R/FR	0.1745 (0.0258)	0.000747 (0.000255)	0.0471 (0.0089)	0.0767	0.00114	67
	High R/FR	0.1240 (0.0227)	0.000102 (0.000057)	0.0393 (0.0136)	0.1399	0.00209	67
Both <i>Khaya</i> and <i>Terminalia</i>							

Table 10.2b: Stomata module : Estimated parameters and errors when the stomata module was fitted to the stomatal conductance data of both species to investigate the effects of growth conditions. Curves drawn from these parameters and those in Table 10.2a can be seen in Fig. 10.1.

Parameter symbols and abbreviations as given in the table.

Low and High R/FR ratio are 0.28 and 1.7 respectively,  
 $g_s$  (light) is the asymptotic stomatal conductance to water vapour in the light ( $\text{mol m}^{-2} \text{s}^{-1}$ );  
 $a_g$  is the initial slope of the stomatal-light response curve ( $\mu\text{mol H}_2\text{O}/\mu\text{mol quanta}$ );  
 $g_s$  (dark) is the dark opening of the stomata; Rss is the residual sum of squares;  
Mse is the mean square error; n are degrees of freedom; () enclose the asymptotic standard deviations at n degrees of freedom.



TABLE 10.3:

Species

R/FR ratio	$\theta$	a	$g_m$	Rd	Rss	Mse	n
<i>Khaya senegalensis</i>							
Low	0.009	0.0933 (0.0197)	0.0351 (0.0024)	0.56 (0.3)	17.85	0.56	32
High	0.58 (0.52)	0.0522 (0.0232)	0.0196 (0.0024)	0.498 (0.28)	12.5	0.4	31
<i>Terminalia ivorensis</i>							
Low	0.265	0.0943 (0.0418)	0.0272 (0.0028)	0.71 (0.31)	15.15	0.49	31
High	0.009	0.0869 (0.0193)	0.0264 (0.0021)	1.13 (0.297)	15.13	0.47	32

Table 10.3: Photosynthesis model: Parameters and errors as estimated from the photosynthesis data by fitting the non-rectangular hyperbola. Curves drawn from these parameters and those in Table 10.4 can be seen in Fig.10.2.

Parameter symbols and abbreviations as given in the table :

Low and High R/FR ratio are growth at 0.28 and 1.70 respectively;  $\theta$  is the convexity Coefficient;  
a is the initial slope of the light response curve (the apparent quantum efficiency  $\mu\text{mol CO}_2/\mu\text{mol quanta}$ );  
 $g_m$  is the mesophyll conductance to  $\text{CO}_2$  ( $\text{mol m}^{-2} \text{s}^{-1}$ ); Rss is the residual sum of squares;  
Mse is the mean square error; n are degrees of freedom; () enclose the asymptotic standard deviation at  
n degrees of freedom.



TABLE 10.4:

Species	R/FR ratio	$g_s$ (light)	$a_g$	$g_s$ (dark)	Rss	Mse	n
<i>Khaya senegalensis</i>	Low	0.157	0.00061	0.0451	2.42	0.76	32
		(0.0354)	(0.00028)	(0.0097)			
	High	0.143	0.00151	0.0244	6.58	2.06	32
		(0.029)	(0.00098)	(0.0195)			
<i>Terminalia ivorensis</i>	Low	0.186	0.0091	0.0488	4.40	1.38	32
		(0.0331)	(0.00044)	(0.0145)			
	High	0.104	0.00061	0.0523	7.10	2.21	32
		(0.038)	(0.00069)	(0.0192)			

Table 10.4: Stomata module: Parameters and errors estimated for the stomatal conductance data by the stomata module. Curves drawn from these parameters and those in Table 10.3 can be seen in Fig. 10.2.

Parameter symbols and abbreviations as given in the table:

- Low and High R/FR ratio are growth conditions at 0.28 and 1.70 respectively;
- $g_s$  (light) is the asymptotic stomatal conductance to water vapour in the light ( $\text{mol m}^{-2} \text{s}^{-1}$ );
- $a_g$  is the initial slope of the stomata-light response curve ( $\mu\text{mol H}_2\text{O}/\mu\text{mol quanta}$ );
- $g_s$  (dark) is the dark opening of the stomata; Rss is the residual sum of squares;
- Mse is the mean square error; n are degrees of freedom;
- ( ) enclose the asymptotic standard deviations at n degrees of freedom.



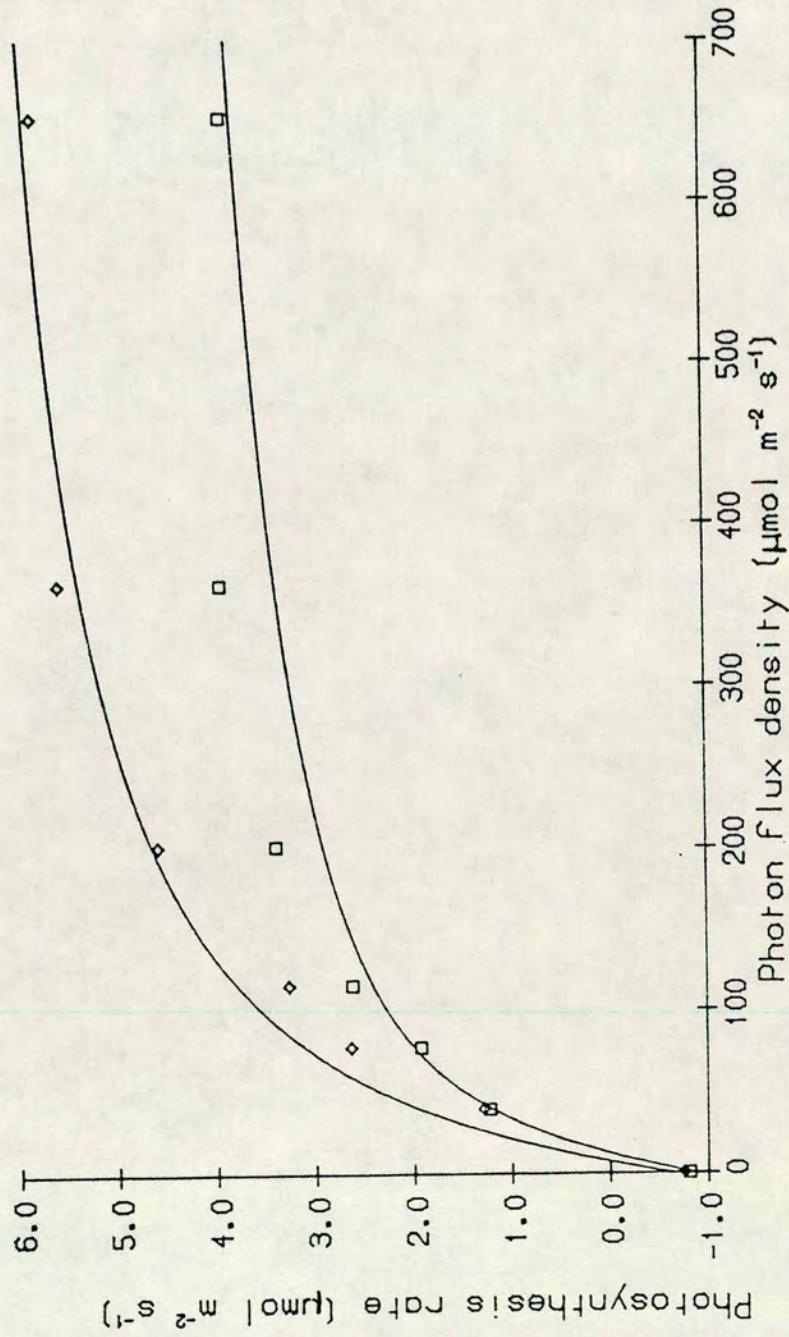


FIGURE 10.1 : The effect of growth at low ( $\diamond$ ) and high ( $\square$ ) R/FR on the photosynthetic response of *Khaya senegalensis* and *Terminalia ivorensis*. Data for both species were pooled as explained in the text. Parameters used in the curve fitting are presented in Tables 10.2a and 10.2b.



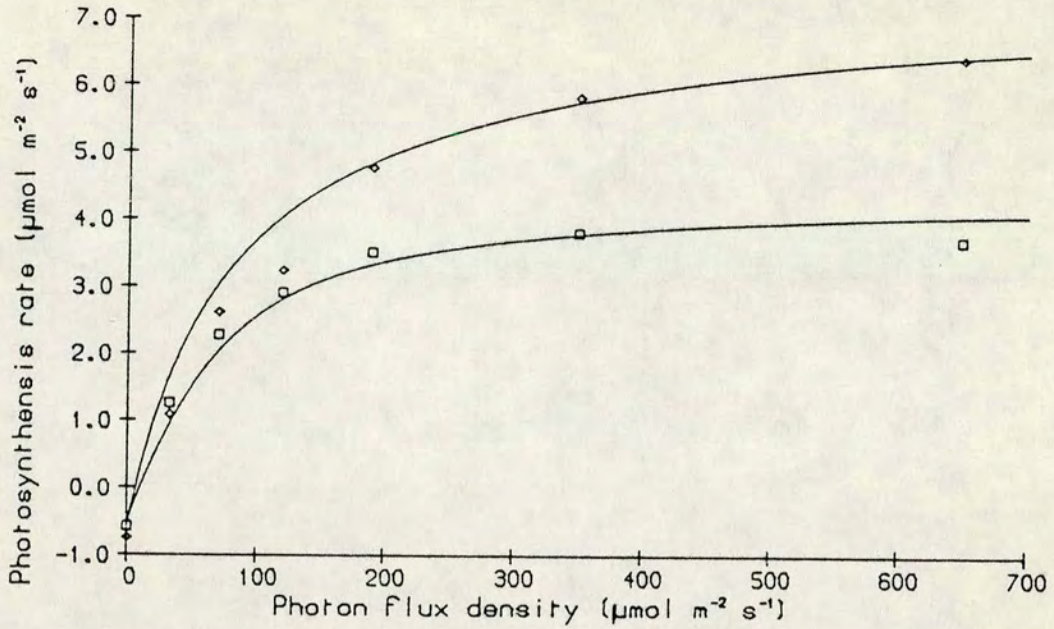


FIGURE 10.2a : The effect of growth at low ( $\diamond$ ) and high ( $\square$ ) R/FR ratio on the photosynthetic response of *Khaya senegalensis*. Parameters used in curve fitting are presented in Tables 10.3 and 10.4.

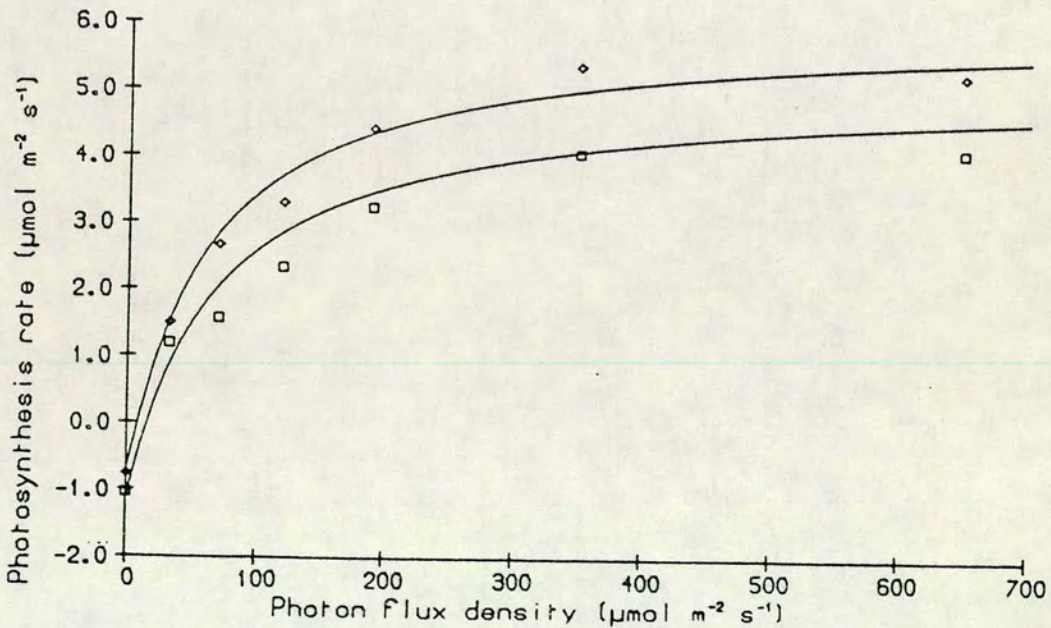


FIGURE 10.2b : The effect of growth at low ( $\diamond$ ) and high ( $\square$ ) R/FR ratio on the photosynthetic response of *Terminalia ivorensis*. Parameters used in curve fitting are presented in Tables 10.3 and 10.4.



### 10.2.2 The influence of R/FR ratio during growth on photosynthetic performance of the two species (on leaf area basis)

Analysis of variance (Appendix Table A6) showed that *Khaya senegalensis* and *Terminalia ivorensis* did not differ in their photosynthetic rates on an area basis. However, the R/FR during growth and the range of photon flux densities imposed during gas exchange measurements showed significant effects on the rates of photosynthesis (Appendix Table A6).

Fitting the photosynthesis model (Table 10.2a) to the pooled data of both species grown at either low or high R/FR ratio and the corresponding stomatal module (Table 10.2b), showed that growth at low R/FR ratio resulted in higher rates of photosynthesis than growth at high R/FR ratio (Fig. 10.1). Moreover, fitting the photosynthesis model (Table 10.3) and the stomatal module (Table 10.4) to the data of each species when grown at low and high R/FR ratio showed that both species responded by an increased photosynthetic performance at low R/FR ratio. Both apparent quantum efficiency and the mesophyll conductance were affected. The increase in maximum rate of photosynthesis was more pronounced in *Khaya senegalensis* (Fig. 10.2a) than in *Terminalia ivorensis* (Fig. 10.2b). *Terminalia ivorensis* displayed higher dark respiration rates when grown at high R/FR ratio than at low R/FR at the same low photon flux density. The magnitudes of respiration rates displayed by *Terminalia ivorensis* were higher than those of *Khaya senegalensis* for both low and high R/FR ratio.

### 10.2.3 The influence of R/FR ratio during growth on the photosynthetic performance, re-expressed on a leaf dry weight

When the photosynthesis rate was re-expressed on a leaf dry weight basis, analysis of variance (Appendix Table A7) showed that species, R/FR ratio during growth, the range of photon flux densities imposed during gas exchange measurements and the interaction of R/FR ratio and species, all had significant effects on the rates of



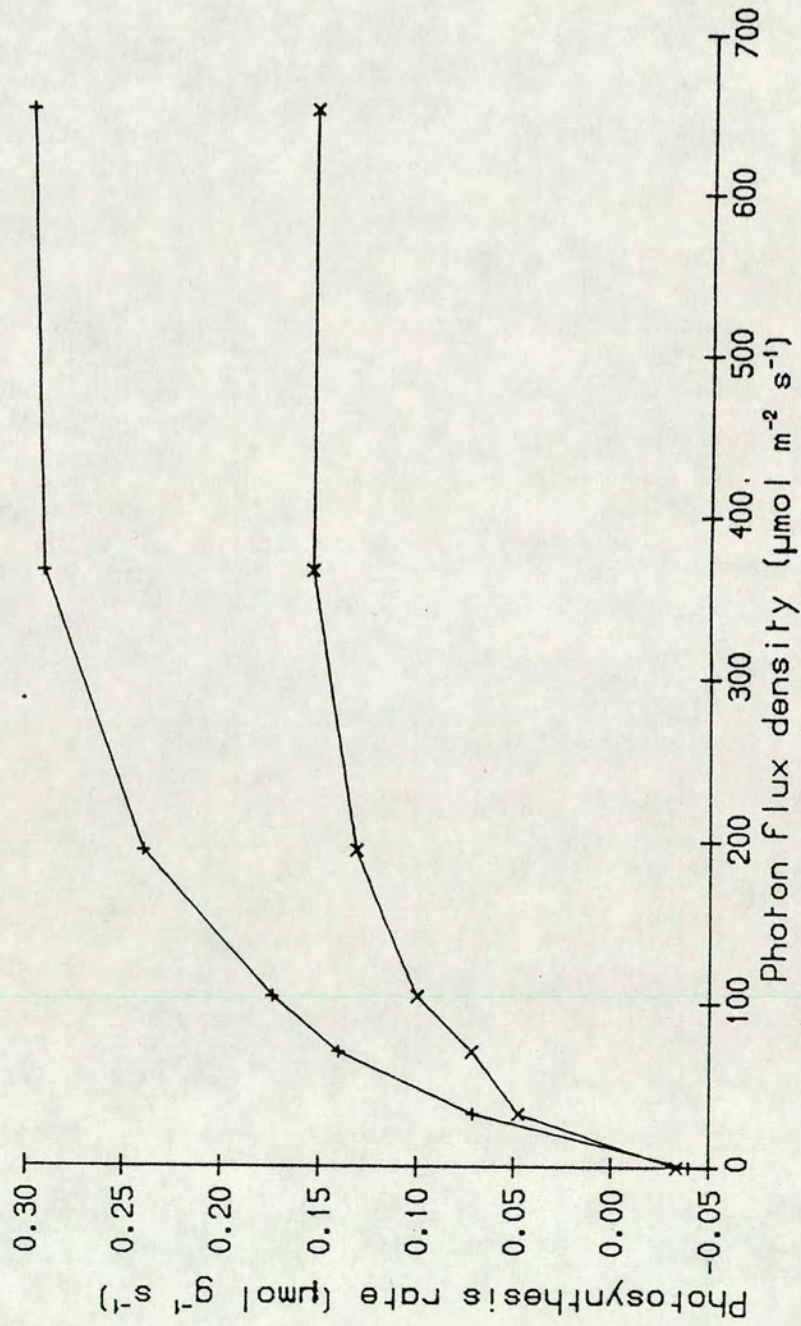


FIGURE 10.3 : The effect of growth at low (+) and high (x) R/FR ratio on photosynthetic response of both species expressed on a dry weight basis. Data for both species have been pooled to investigate the general effect of low or high R/FR ratio as explained in the text.



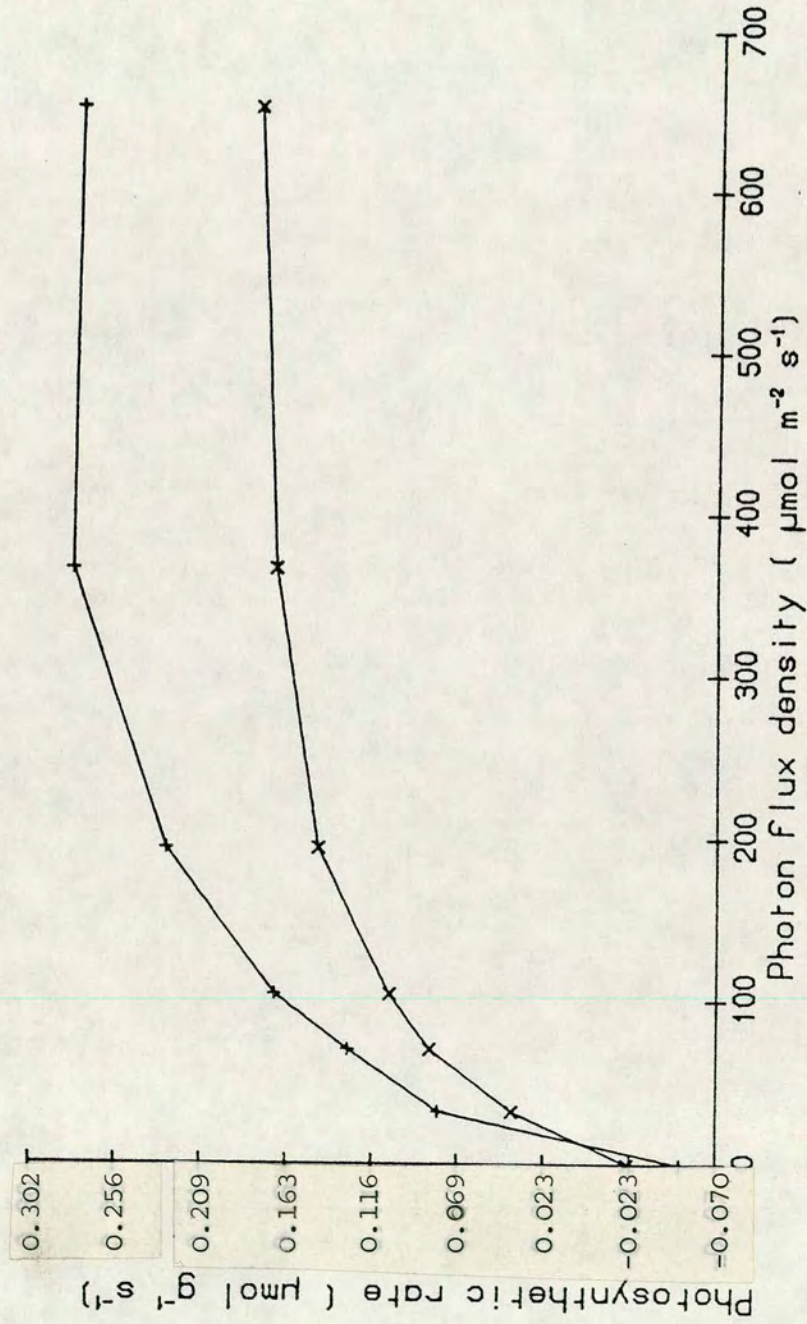


FIGURE 10.4 : The effect of R/FR ratio on photosynthetic response of *Terminalia ivorensis* (+) and *Khaya senegalensis* (x) expressed on a dry weight basis. Data for each species for growth at low or high R/FR were pooled as explained in the text.



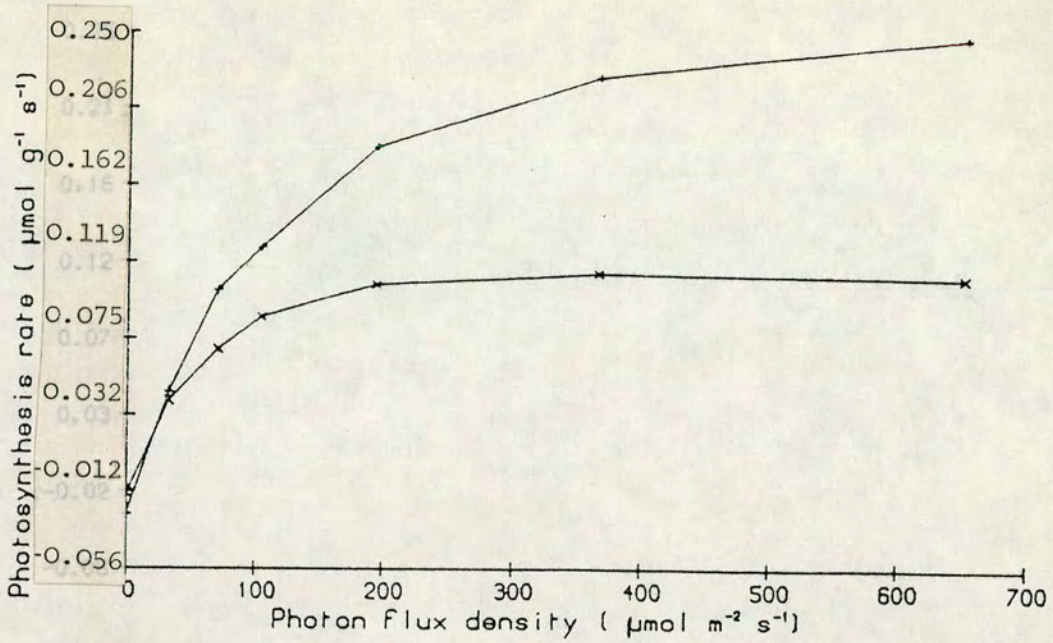


FIGURE 10.5a : The effect of growth at low (+) and high (x) R/FR ratio on photosynthetic response of *Khaya senegalensis* expressed on a dry weight basis.

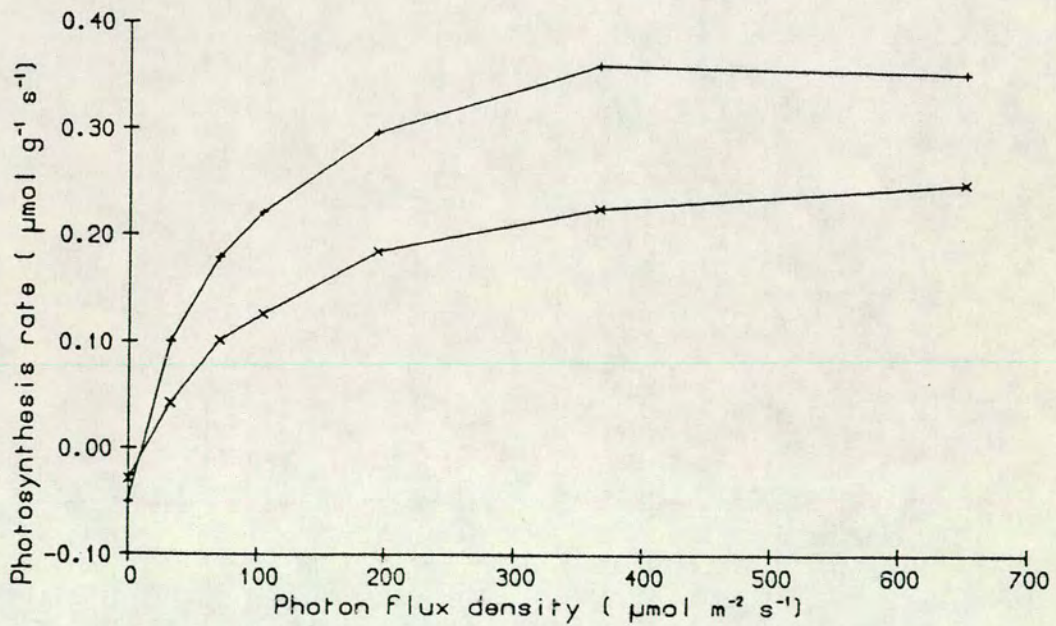


FIGURE 10.5b : The effect of growth at low (+) and high (x) R/FR ratio on photosynthetic response of *Terminalia ivorensis* expressed on a dry weight basis.



photosynthesis.

When the pooled photosynthesis data for both species at either low or high R/FR ratio are expressed on a weight basis, again growth at low R/FR resulted in higher photosynthetic performance than growth at high R/FR ratio (Fig. 10.3). This is similar to the conclusion already shown on an area basis (Fig. 10.1). However, the influence of specific leaf area (Table 10.1) on species performance was clearly evident when data for growth at high and low R/FR ratio of each species were pooled (Fig. 10.4). It was *Terminalia ivorensis* which showed a higher SLA (Table 10.1) and it also showed a higher photosynthetic rate and dark respiration rate on a leaf dry weight basis than *Khaya senegalensis* (Fig. 10.4). Moreover, the influence of specific leaf area was more pronounced in *Terminalia ivorensis* (Fig. 10.5b) than in *Khaya senegalensis* (Fig. 10.5a). It was *Terminalia ivorensis* (Fig. 10.5b) which displayed higher rates of photosynthesis and dark respiration when grown at low R/FR ratio than the corresponding rates in *Khaya senegalensis* (Fig. 10.5a).

### 10.3 Discussion

So far, investigations into the effect of R/FR ratio on growth have concentrated on morphogenesis. There appears to be only one publication in which the photosynthetic attributes of leaves have been studied in relation to R/FR (Corré 1983b); and that work does not concern tree species but herbs. Moreover, the author considered the photosynthetic response only in a restricted range of photon flux density, viz. 0 to  $220 \mu\text{mol m}^{-2} \text{s}^{-1}$ . He found that red/far-red ratio during growth exerted no measurable influence on the rate of photosynthesis, although dark respiration was affected in some species.

In the present work, there appears to be a clear indication that red/far-red ratio during growth does affect photosynthetic attributes through its effects on the apparent quantum efficiency and mesophyll conductance. Dark respiration rates may be affected (e.g. Corré, 1983b) but in the present work, because of some uncertainty in the correction factor (Section 8.1.5) it would be unwise to attach much



importance to small apparent differences. There may however be an effect on *Terminalia ivorensis*.

As shown in Table 10.3, the apparent quantum efficiency and mesophyll conductance were higher at low R/FR ratio than at high R/FR ratio and this was more pronounced in the shade tolerating *Khaya senegalensis* than in the light demanding *Terminalia ivorensis*; so was the photosynthetic rate on an area basis (compare Figs. 10.2a with 10.2b). It is worth noting that the direction of this response is in contrast to that reported in the previous chapter. In those experiments, the light regimes during growth were achieved with neutral filters, so that the 'shade' treatment did not differ in its spectral distribution from the 'sun' treatment. We may conclude that the two components of vegetational shade, i.e. reduced PAR and reduced R/FR produce distinct and quite different responses as far as the photosynthetic characteristics of the leaf are concerned.

High apparent quantum efficiency and mesophyll conductance under a low R/FR ratio might be important adaptation characteristics of shade tolerant species like *Khaya senegalensis* during growth under the dense shade of the understorey; as these enable the plant to utilize the available PAR more efficiently.

Let us suppose that when *Khaya senegalensis* experiences a photon flux density of  $125 \mu\text{mol m}^{-2} \text{s}^{-1}$  it is a small sapling in the C or D layers (see Section 2.1 and also refer to Smith 1962, Longman and Jeník 1974). The only sources of such light are : unfiltered daylight which has passed through holes in the canopy such as sunflecks; and attenuated daylight, the spectrum of which has been altered by the canopy foliage through the processes of absorption, reflection and transmission (see Section 2.5, 2.5.1 and 2.5.2). However, seedlings and saplings in the understorey experience filtered or attenuated light regimes of low PAR and R/FR during most of the day although sunflecks may contribute a significant portion of daily photon flux density available for photosynthesis (e.g. Pearcy 1983). Sunflecks depend on the proportion of the visible solar disk at any given hole in the canopy as well as its duration, and these sunflecks are highly variable because



they are influenced by the prevailing weather conditions (e.g. cloud cover and rainy season). Hence the most important source of photosynthetically active radiation appears to be that attenuated by the canopy foliage, which has a low R/FR component. If the species is to survive in these conditions, it must develop the capacity to photosynthesise rapidly in the dim light and also to exploit brief periods of bright light from sunflecks. The data suggests it does both these.

If on the other hand light demanding species such as *Terminalia ivorensis* were to be put under such conditions, we may (from work described in previous chapters) expect it to channel all its assimilates towards energy demanding processes, in particular increased extension growth and leaf area expansion. In its preferred habitat, more open places, it would thus outgrow competitors by raising its leaves above theirs.

In the process of natural selection, a high rate of photosynthesis in *Terminalia* or any other light demander might not have such a strong selective advantage as growth *per se*. For the shade tolerator in the dim layer, a high rate of photosynthesis would be very strongly selected for, whereas a growth response in dim light might be selected against.

There are just two reservations in the conclusions outlined above. They relate to the action spectrum of photosynthesis in relation to that of the quantum sensor.

The experimental aim of this part of the work was to maintain plants at a constant and low PAR whilst varying the red/far-red ratio. Although this was apparently achieved it should be recognised that PAR in these experiments as measured by a quantum sensor may not be an appropriate measure of photosynthetically active radiation. It is known that plants vary in their sensitivity of the photosynthetic apparatus to radiation of different wavelength (Rabinowitch, 1951). It is also well known that different leaves have different absorptances of PAR (e.g. Gaastra, 1959).



Thus, although Gaastra (1959) assumed that the quantum yield of photosynthesis was independent of wavelength over a range of 400 - 700 nm, McCree (1981) pointed out that the relevant quantity is the yield per absorbed quantum; and to calculate this quantity, it is necessary to measure both yield per incident quantum and the spectral absorptance of the leaf. McCree (1981) cites Björkman's work (1968) reporting measurements of the spectral quantum yield of photosynthesis in leaves of three species grown under controlled environment conditions. The quantum yield was found to be 0.074 mol CO<sub>2</sub> per mol quanta absorbed between 670 and 540 nm, decreasing to 0.062 between 520 and 450 nm; and rapidly decreasing at wavelengths greater than 670 nm. The data did not cover the whole of the photosynthetically active waveband. Later, McCree (1972a) and McCree and Keener (1974) measured the quantum yield for all wavelengths that are photosynthetically active (350 - 750 nm). In all cases, the spectral quantum yield curve showed two broad maxima, centered at 620 and 440 nm, with a "shoulder" at 670 nm.

In the present experiment, the reduction of R/FR ratio was achieved by use of green cinemoid filters. Leaves are known to absorb relatively little in the green part of the spectrum, yet a quantum sensor still senses the photons that the eye perceives as green. Thus, because of its response characteristics, under the green cinemoid material the sensor will tend to over-estimate the photons which are actually available for photosyntheses. Overall, this means that the low red/far-red treatment must have had a somewhat lower flux density of photosynthetically active photons than that of the high R/FR treatment.

Finally, although the relative contribution to photosynthesis of quanta above 700 nm is thought to be insignificant as it lies outside the range of absorption of chlorophylls (e.g. Wooley 1971); Björkman (1973) suggested that these quanta may be important in the photosynthesis of extreme shade plants. McCree (1981) estimated that the region above 700 nm might account for as much as 7 % of the total quantum flux density available for photosynthesis. However, since virtually nothing is known about the photosynthetic action spectra of tropical tree species in their natural habitats, it is still impossible to



determine the importance of the quanta above 700 nm in photosynthesis of such plants as found in the dim layer. Nevertheless, the detection of vegetational shade-light and its perception by the plant has been shown to result into morphogenetic responses that differ between species.



## CHAPTER 11

### *SUMMARY, GENERAL DISCUSSION AND IMPLICATIONS*

#### 11.1 Influence of light regime during growth

The present experiments have confirmed that many of the conclusions made in the literature regarding the response of plants to shade, based on observations on herbaceous crops and temperate trees, generally hold for tropical timber trees. It has, moreover, been possible to separate the effects of a reduced photon flux density *per se* from those of a reduced photon flux density coupled with a low red/far-red ratio.

1. Plants adjusted to shade in several ways. One of the most important of these seemed to be the increase in specific leaf area that occurred when leaves had been formed at low photon flux densities. It was through this increase in specific leaf area that the leaf area ratio was increased, hence counteracting the low net assimilation rates that inevitably occurred in deep shade. A new finding in the present work was that the specific leaf area is sometimes affected strongly by the red/far-red ratio. This response deserves further attention in the future.

2. Other adjustments to shade involving extension growth and development were species-dependant varying with the ecological characteristics of the tree. These will be considered in the next section.

3. The photosynthetic characteristics of the leaves also depended on the light regime in which the leaves had developed. The parameters of the light response model were calculated as a means of comparing these characteristics. In general, leaves developed at low photon flux densities displayed low stomatal and mesophyll conductances. As a consequence their maximum rates of photosynthesis were lower than when the leaves had been grown in bright conditions. The photosynthetic performance at very low photon flux densities, such as



those prevailing on the forest floor, depends critically on the initial slope of the light response curve (determined largely by the fundamental quantum efficiency) and on the dark respiration rate. These two parameters, like the specific leaf area mentioned above, were found to be not only affected by a reduction in the photon flux density: they were considerably influenced by the red/far-red ratio that accompanied this reduction. At the low red/far-red ratio the initial slope of the light response curve was steeper.

4. Although it has been possible to simulate two main features of forest shade, namely the reduction in photon flux density with or without an appropriate reduction in the red/far-red ratio, the large variations in energy that occur as a result of sunflecks are more difficult to simulate. Experiments involving a stepwise change in photon flux density do however suggest an underlying complexity involving synthesis and degradation of the light harvesting system. The speed of this response in relation to the occurrence of sunflecks and its implications for photosynthesis have not been addressed in the present work, but may be of great importance in understanding the carbon economy of seedlings in forest conditions.

## 11.2 Influence of the ecological characteristics of the species

As far as it is possible to rank the species in terms of their distribution in the forest and in clearings, based on the literature on forest succession, it is clear that *Khaya senegalensis* is a shade-tolerator occurring in the late stage in succession. Both species of *Terminalia* occur at an early stage in succession and they have characteristics of pioneer species. *Triplochiton scleroxylon* appears to be intermediate.

The relationship between ecological characteristics and physiological responses based on these comparisons appear as follows :-

1. The light demanding *Terminalia ivorensis* failed in the shade because the photosynthetic rate at low photon flux densities (preliminary glasshouse experiment) was inadequate to maintain a positive



carbon balance. Moreover, growth of the stem continued despite a negative carbon balance, leading eventually to leaf abscission and mortality of some of the plants. The shade tolerant *Khaya senegalensis* on the other hand maintained a positive carbon balance, did not lose its leaves and set bud; indicating slow growth and a conservative use of assimilates.

2. Whereas both species responded to a reduced photon flux density and low red/far-red ratio by increasing specific stem length, the light demanding *Terminalia ivorensis* showed other developmental characteristics that were not observed in *Khaya senegalensis*. In particular, *Terminalia ivorensis* responded to low photon flux density with low red/far-red ratio by producing large but very thin leaves. Leaf area ratio and specific leaf area were about 10 times higher than the leaves produced under low photon flux density with a high red/far-red ratio. As regards specific leaf area, *Terminalia ivorensis* showed sensitivity to red/far-red ratio that was not observed in *Khaya senegalensis*.

3. There were only minor differences between species in chlorophyll content : when grown in dim light, all species increased their chlorophyll synthesis, and transfer from dim light to bright light resulted in chlorophyll decomposition of up to 50 %.

4. When grown at a range of photon flux densities, *Khaya senegalensis* never displayed maximum rates of photosynthesis greater than  $4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  whereas the light demanding species if grown at high photon flux densities adjusted to them and attained rates of about twice this value. However, maximum photosynthesis in *Khaya senegalensis* was observed to exceed  $4 \mu\text{mol m}^{-2} \text{ s}^{-1}$  when the low photon flux regime was accompanied by a reduction in the red/far-red ratio. In these conditions presumably like those found in the dim layer of the forest, the maximum rates could be as high as  $6.4 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . This may be interpreted as adaptation to utilize effectively the radiation in sunflecks. These ecological aspects will be considered in the next section.



The species also differed in their light compensation points. The reason for failure of *Terminalia ivorensis* in the initial glasshouse experiment is clear when the light compensation points are compared. In *Terminalia ivorensis* the value is  $25 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$  whereas in *Khaya senegalensis* the corresponding value was 10.

5. On an area basis, respiration rates were always low when plants were grown at low photon flux density. When *Khaya senegalensis* was grown at high photon flux density its respiration rate was higher than all the other tree species.

In terms of carbon economy, it is perhaps useful to consider respiration rates on a weight basis. *Khaya senegalensis* has the lowest respiration rate, achieved at low photon flux density, and the ranking of dark respiration rates seems to reflect the ecological status of species i.e. from shade tolerant to light demanding we have *Khaya senegalensis* < *Triplochiton scleroxylon* < *Terminalia ivorensis* = *Terminalia superba*.

6. *Cyperus papyrus* displayed totally different characteristics from all the trees, with higher stomatal and mesophyll conductances and consequent higher photosynthetic rates. It fails in the shade because of its very high respiration rates and compensation point of  $70 \mu\text{mol m}^{-2} \text{ s}^{-1}$ .

### 11.3 Absolute rates of photosynthesis of tropical trees

Woody plants differ from herbaceous species in displaying low relative growth rates (Jarvis and Jarvis, 1964; Okali, 1971); low unit leaf rates (Whitmore and Gong-Wooi-Khoom, 1983) and low rates of photosynthesis (Larcher, 1975).

Very little is known about the photosynthetic rates of tropical trees. What information there is (Larcher, 1969; Synnott, 1975; Osonubi and Davies, 1980; Koyama, 1981; Longenheim et al 1984) suggests that maximum photosynthetic rates are lower than those known to occur in many tropical herbs; and are similar to those of temperate trees. Data



from various studies on  $C_3$  trees (see Larcher, 1975, Table 3.4, page 95) shows that the maximum rates of photosynthesis lie within a broad range of  $2 - 16 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  whereas those of  $C_4$  tropical grasses are higher  $18-50 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ .

Koyama (1981) working with excised leaves, reported differences in photosynthetic capacities in leaves of diverse form in the tropical moist forests of <sup>the</sup> Malayan peninsula as summarized below (Table 11.1).

Koyama's rates are substantially higher than any of those from tropical trees reported subsequently.

Growth form	Maximum photosynthetic rate $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	Light saturation point $\mu\text{mol m}^{-2} \text{ s}^{-1}$	Light compensation point $\mu\text{mol m}^{-2} \text{ s}^{-1}$
Upper canopy: sun type	12.6 - 18.9	250 - 370	12
shade type	6.3 - 9.5	125 - 185	6 - 12
Lower canopy: shade type	4.4 - 5.0	125	6 - 12
Secondary forest	12.6 - 15.8	125 - 245	6 - 12
Climbers	12.6 - 18.9	125 - 245	6 - 12
Ground herbs	1.3 - 1.9	25 - 37	2.6 - 6

TABLE 11.1 Adapted from Koyama (1981), determinations made at a chamber temperature between  $26 - 30^\circ \text{C}$ .

Under a variety of field conditions, Mooney *et al* (1984) reported data for a range of Mexican species of *Piper* including shrubs and trees. The mean maximum photosynthetic rates were between  $3.4 - 8.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  at light saturation ( $\approx 300 - 400 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ).

The results of the present experiments have been compared to those of Langenheim *et al.*, (1984) for glasshouse-grown *Caesalpinoids* and *Agathis* species at 6 % shade and 100 % full sunlight (Table 11.2).



TABLE 11.2 Maximum photosynthesis rates and compensation points. The figures in parentheses indicate values obtained when the red/far-red was low (see Chapters 9 and 10).

Ecosystem	Species	Photosynthetic rates at		Light compensation point	
		saturation		point	
		$(\mu\text{mol m}^{-2}\text{s}^{-1})$		$(\mu\text{mol m}^{-2}\text{s}^{-1})$	
		Sun	Shade	Sun	Shade
Seedlings of emergent trees in the Amazonian lowland rainforest canopies (Langenheim et al 1984)	<i>Caesolpinoids</i>				
	<i>Copaifera venezuelana</i>	7.5	7.0	15	8
	<i>Hymeneae</i>				
	<i>courbaril</i>	5.0	4.0	15	9
	<i>Hymeneae parviflora</i>	3.0	3.6	13	9
Tropical Australian semi-evergreen rainforest (Langenheim et al 1984)	<i>Araucaria</i>				
	conifers				
	<i>Agathis microstacyta</i>	4.5-5.0	3.5	24	5
	<i>Agathis robusta</i>	7.5-10	3.5	23	15
West African tropical forest timber trees as reported in the present study.	<i>Terminalia</i>				
	<i>superba</i>	8.5	4.5	16	8
	<i>Terminalia ivorensis</i>	8.0	3.8(5.6)	25	25(9)
	<i>Triplochiton scleroxylon</i>	9.4	4.0	15	10
	<i>Khaya senegalensis</i>	4.2	3.5(6.6)	20	10(5)



Lagenheim *et al* (1984) reported that *Hymeneae parviflora* is more slow growing than *Hymeneae courbaril* which grows vigorously when small or medium sized gaps occur in the canopy; and that *Agathis robusta* regenerates rapidly in large gaps or clearings when small or medium gaps occur in the canopy. Table 11.2 shows that the values of shade leaves and species compare well to those of *Khaya senegalensis* and other slow- growing trees whilst those of the sunleaves and fast growing, light demanding, species are also in close agreement with data on light demanding trees in the present study.

Ladipo *et al* (1984) reported rates for six clones of *Triplochiton scleroxylon*: the rates of photosynthesis at light saturation ranged from  $4.5 - 7.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  which are comparable to those reported in the present study (Table 11.2).

It is likely that the maximum rates of photosynthesis reported in the literature for tropical trees may have an adaptive significance and this may be related to the light environment as experienced under canopies of tropical moist forests (see Chapter 2). The photosynthetic response of plants to the remarkably low light levels, which characterize the rainforest floor, has been studied in some detail (Björkman *et al* 1972; Pearcy, 1983; Pearcy and Calkin, 1983). Björkman and Ludlow (1972) found that the amount of photosynthetically active radiation (400 - 700 nm) at the bottom of a Queensland rainforest was exceedingly low (see section 2.4). Diffuse photon flux density amounted to only about  $5 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ; whereas at the top of the canopy, over  $2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$  was measured during midday. Over half of the clear day radiation reaching the forest floor occurred during brief periods of sunflecks. To survive in these conditions, leaves require low light compensation points but also need high maximum rates of photosynthesis if they are to make best use of the sunflecks.

Nearly half of the total carbon gain of an understory herb *Alocasia macrorrhiza* occurred during these brief periods of sunflecks (Björkman *et al*, 1972). In Hawaii, Pearcy and Calkin (1983) in a detailed study of the carbon balance of the understory sapling of a  $\text{C}_3$  tree *Claoxylon sandwicense* demonstrated that this species attains light



saturated photosynthesis rates during natural sunfleck periods. They also found that the growth rate of individuals of *Claoxylon sandwicense* in the understory is directly related to the potential duration of sunflecks it receives.

When shade is coupled with a low red/far-red ration, the present study suggests that shade plants may demonstrate a relatively high photosynthesis rate. This is evident in the response of *Khaya senegalensis* at low red/far-red ratio relative to the rate at the same photon flux density with a high red/far-red ratio (Table 11.2). Low red/far-red ratio is typical of vegetational shadelight (see section 2.5) that has most of its wavelengths useful for photosynthesis attenuated by the canopy foliage. The ability to increase photosynthetic capability under such conditions of low photon flux density with a low red/far-red ratio may be very important in utilization of sunflecks and consequent adaptation of shade species to the prevailing light regime by maintaining a positive carbon balance.

#### 11.4 Resistance to CO<sub>2</sub> transfer

The process of CO<sub>2</sub> transfer between the ambient air and the sites of carboxylation is frequently modelled as a chain of resistances ( $r$ ), following the original scheme of Gaastra (1959) but developed as outlined by Farquhar and Shakey (1982). Thus according to Gaastra (1959):

$$F = \frac{C_a - C_c}{r_a + r_s + r_m} \quad 11.1$$

where:

$F$  is the CO<sub>2</sub> flux

$C_a$  is the ambient CO<sub>2</sub> concentration

$C_c$  is the CO<sub>2</sub> concentration in the chloroplasts

$r_a$ ,  $r_s$  and  $r_m$  are aerodynamic, stomatal and mesophyll resistances, respectively.



The mesophyll resistance is a residual term which embraces several processes. Subsequent workers have sometimes preferred to separate a carboxylation resistance. Thus, according to Farquhar and Sharkey (1982) :

$$F = \frac{C_a - C_c}{[r_a + r_s + r_m + r_x]P} \quad 11.2$$

where

$r_x$  is the carboxylation resistance

$P$  is the atmospheric pressure

Although undoubtedly a gross simplification, the benefit of this analysis is that it enables statements to be made regarding the control of photosynthesis by environmental, anatomical and biochemical factors. Recently, several studies suggest that tropical trees may differ from temperate trees in the magnitudes for transfer of  $CO_2$  and water vapour (Grace, Okali and Fasehun 1982; Osonubi and Davies 1980).

The aerodynamic resistance ( $r_a$ ) depends on the size and shape of the leaf and the wind speed. Its value in tropical trees is frequently much higher than in temperate trees, simply because the leaves are generally larger in tropical species. In most large-leaved species, at low windspeeds ( $0.1 - 1 \text{ m s}^{-1}$ ) the resistance is likely to be much higher than in temperate trees and around  $4 \text{ s cm}^{-1}$  (Grace, Fasehun and Dixon, 1980). In experimental studies on photosynthesis such as those presented in this thesis, the aerodynamic term is, for convenience, deliberately made small by stirring the air around the leaf in the assimilation chamber, but its magnitude in natural conditions of low flow cannot be ignored when considering possible photosynthetic rates in the field.

The stomatal resistance depends on the number and dimensions of the stomatal pores. Pore aperture is influenced by environmental conditions, most notably the prevailing photon flux density and water status of the leaf. On the magnitudes of this resistance in tropical



trees, there is presently no real consensus. Very low resistances have been reported by Grace *et al* (1982) in *Tectona grandis* and *Gmelina arborea* growing in the field. Other workers have found resistances which, although rather low compared with temperate species, are not as low as those in Grace *et al* (1982) (see Table 11.3). In water stressed plants this resistance can be quite high (Osonubi and Davies, 1980).

The mesophyll (or intercellular) resistance is a complex term that includes a liquid-phase transport component and an enzyme component that depends on the activities of biochemical and photochemical processes. It is influenced by the internal anatomy of the leaf, including the leaf thickness and the carboxylation activity. Ludlow and Jarvis (1971) considered the mesophyll resistance ( $r_m$ ) to be made up of at least three components : an excitation resistance ( $r_e$ ) important only at low photon flux densities when photosynthesis is limited by the photochemical partial process; a largely physical resistance to transfer of  $CO_2$  in the liquid phase ( $r_m$ ) from the Liquid-air interface to the site of primary carboxylation of photosynthesis; and the carboxylation resistance ( $r_x$ ) inversely proportional to the activity of the carboxylating enzymes.

When available data are assembled (Table 11.3), it becomes clear that despite the high aerodynamic resistance implied by the large size of leaf, the limiting resistance for  $CO_2$  transfer is most likely to be the mesophyll resistance, this value being high in relation to  $r_a + r_s$ , except in water stressed plants where  $r_s$  becomes high.

In this study we have shown that the light regime during growth induces considerable variation in mesophyll resistance. Other studies e.g. on maize by Chartier *et al* (1977) showed that decreased mesophyll resistance of the high light grown leaves was accounted for by the large increases in the mesophyll cell surface area per unit leaf surface. Nobel *et al* (1975) showed that the differing light saturated photosynthetic rates of leaves grown at different photon flux densities reflected the variation in  $A_{mes}/A$ . Holmgren *et al* (1965) also reported lower mesophyll resistances in sun than shade plants and showed that



TABLE 11.3 : EXAMPLES OF RESISTANCES IN TROPICAL SPECIES

TYPE OF RESISTANCE	SOURCE	EXPERIMENTAL MATERIAL AND CONDITIONS	VALUES mol <sup>-1</sup> m <sup>2</sup> s
Boundary layer r <sub>a</sub>	Grace <i>et al.</i> (1980) The LI-1600 porometer	Brass model leaves of <i>Triplochiton scleroxylon</i> , <i>Tectona grandis</i> , and <i>Gmelina arborea</i> (17 °C) Assumes a fixed boundary layer resistance	0.075-9.98 0.378
Stomatal resistance r <sub>s</sub>	Osonubi and Davies (1980) Grace <i>et al.</i> (1982) Ladipo <i>et al.</i> (1984) Mooney <i>et al.</i> (1984) This study (Table 9.6, values in the light) (Refer to Table 10.4 values in the light) Pearcy and Calkin (1983)	Water stressed <i>Gmelina arborea</i> (16 hrs, 20 °C in relation to VPD) <i>Gmelina arborea</i> and <i>Tectona grandis</i> during wet season in Nigeria (30 °C) 6 clones of <i>Triplochiton scleroxylon</i> (28 °C) <i>Piper hispidum</i> . Field measurements at different relative humidities <i>Terminalia superba</i> , HPD-LPD <i>Khaya senegalensis</i> , LPD-HPD <i>Triplochiton scleroxylon</i> , HPD-LPD <i>Terminalia ivorensis</i> , HPD-LPD <i>Cyperus papyrus</i> , HPD <i>Khaya senegalensis</i> , Low-High R/FR <i>Terminalia ivorensis</i> , Low-High R/FR Endemic species in Hawaii <i>Euphorbia forbesii</i> (C <sub>4</sub> ) <i>Claoxylon sandwicense</i> (C <sub>3</sub> ) Leaf resistance (23 °C)	38.83 1.59-7.5 4.79-8.31 0.9-10 2.74-6.06 5.43-6.80 3.41-5.02 2.63-4.24 1.29 6.37-6.99 5.38-9.61 15.87 10
Mesophyll resistance r <sub>m</sub>	Pearcy and Calkin (1983) Ladipo <i>et al.</i> (1984) This study (refer to Table 9.1) This study (Table 10.3)	<i>Euphorbia forbesii</i> <i>Claoxylon sandwicense</i> 6 clones of <i>Triplochiton scleroxylon</i> <i>Terminalia superba</i> , HPD-LPD <i>Khaya senegalensis</i> , HPD-LPD <i>Triplochiton scleroxylon</i> · HPD-LPD <i>Terminalia ivorensis</i> , HPD-LPD <i>Cyperus papyrus</i> HPD <i>Khaya senegalensis</i> , Low-High R/FR <i>Terminalia ivorensis</i> , Low-High R/FR	14.49 58.82 37.78-70.53 27.86-50.5 41.32-66.67 19.42-57.47 25.06-63.29 10.8 28.49-51.02 36.76-37.87

TABLE 11.3:  
Abbreviations: HPD and LPD are high and low photon flux density respectively.  
R/FR ratio is red/far-red ratio.  
VPD is vapour pressure deficit.  
The conversion factors are given by Jones, (1983, p.277).



photosynthesis in shade plants seem to have been limited by interaction of limiting factors whereas in the sun species the transfer of  $\text{CO}_2$  to the carboxylation sites appeared to be the dominant factor. Ludlow and Jarvis (1971) suggested that in conifer needles the liquid-phase  $\text{CO}_2$  transfer resistance may be more important than in broad leaves because of the densely packed arrangements of large mesophyll cells within a comparatively small cross-sectional area of intercellular spaces available for gaseous diffusion.

Ladipo et al (1984) found that genetic variation in photosynthesis within the tropical tree *Triplochiton scleroxylon* was explicable in terms of variation in mesophyll resistance which was very large in relation to stomatal resistance at high photon flux densities. A similar conclusion was reached by Langenheim et al (1984) who reported that the lack of response of light saturated photosynthesis to photon flux density during growth was not due to stomatal limitation. As shown in Table 11.3, it is possible that the differences in photosynthetic rates between species are more related to the prevailing light regime during growth and subsequent magnitudes of mesophyll resistances.

### 11.5 Dark respiration rates in tropical trees

Recent studies on tropical hardwoods suggest that the carbon balance of trees in warm climates may be dominated by high respiratory fluxes. According to Larcher (1975), the high biomass supported by the wetter forests evidently results in a high respiration load. About 80 % of the gross productivity is said to be respired in wet forests, whilst this figure falls to about 40 % in the subtropical dry forests, a value more typical of temperate deciduous forests.

Without going further into productivity studies, short term laboratory experiments on tropical tree seedlings have shown that indeed respiration rates are higher for sun leaves than shade leaves. This is reflected in their light compensation points too. In this study, it was demonstrated how the respiration rate on a weight basis, in particular the ratio of  $R_{\text{LPD}}/R_{\text{HPD}}$  appears to be related to the ability



to tolerate shade. On this basis, *Khaya senegalensis* showed a lower value of  $R_{LPD}/R_{HPD}$  than the light demanders.

In Chapter 7, it was shown that seedlings of *Cyperus papyrus* died within one week when grown at  $40 \mu\text{mol m}^{-2} \text{s}^{-1}$  and in Chapter 9 it was shown that the light compensation point of such plants was  $70 \mu\text{mol m}^{-2} \text{s}^{-1}$ . In Chapter 5, it was also shown that *Terminalia ivorensis* was below its light compensation point under the deepest shade. It lost its leaves, its relative growth rate and net assimilation rate became negative and these resulted in eventual death of the seedlings. *Khaya senegalensis* was able to maintain a positive carbon balance as a result in part of its lower rates of respiration. In all these studies it should be borne in mind that the respiration rate would be higher (more negative), and the light compensation point higher, if the whole plant - including stems and roots - were being considered.

Fasehun and Audu (1980) reported the leaf respiration rates of light demanding tropical hardwoods: *Gmelina arborea*, *Terminalia superba*, *Terminalia ivorensis* and *chlorophora regia*. They showed that leaf respiration rates were inversely related to the total dry mass after 12 weeks of growth. The species with least respiratory losses showed most growth whilst those with highest respiration rates showed the poorest growth. A similar conclusion may be drawn from data of Ladipo *et al* (1984).

It seems respiration plays an important role in the growth of tropical trees and is higher for light demanders than shade tolerators in their natural habitat or in the laboratory. Adaptation to shade usually involves capacity to develop a low respiration rate.

### 11.6 Ecological implications

A physiological explanation relating to the growth, survival and distribution of light demanding and shade tolerating tropical trees species cannot be advanced on the basis of simple, short term duration, controlled environment experiments, such as described here. The influence of shade on seeds, for example, was not thoroughly



investigated and the number of species investigated were very few, only one shade tolerant species being available. Besides, extrapolating the results from investigations in controlled environments to field conditions is fraught with difficulty. Whereas in controlled environments some variables can be controlled and one of particular interest investigated; under field conditions, the variables fluctuate and interact together and influence the plant in a complicated way. Moreover, artificially simulated environments may fail to represent important features of field conditions. Nevertheless, the data from these experiments contribute to an understanding of gross ecological phenomena such as secondary succession.

#### 11.6.1 Secondary succession in tropical moist forests

The process of secondary succession in tropical moist forests is not yet fully understood because of limited research as yet carried out in these more complicated ecosystems than those of temperate forests. The information available is not enough to construct models of secondary succession or explain the apparently random distribution of tree species in these forests. Denslow (1978) pointed out that "understanding processes of secondary succession must come primarily from an appreciation of the variation in adaptive strategies of these species, as this will lead eventually to enlightened management of the rapidly dwindling tropical moist forests". At the moment, the pattern and process of secondary succession still appears intricate in tropical moist forests.

Secondary succession is a process of species replacement in canopy gaps or stimulation of growth of suppressed species under the canopy whenever such gaps occur above them and it is believed that light is one of the main environmental variables directly influencing this process besides those which create such gaps (see Section 2.2).

According to Whitmore (1983) the forest canopy is continually changing as trees grow up, die and are replaced in canopy gaps. Seedlings which grow up in small gaps are those which were already present before such gaps occurred and had become established in the



undergrowth shade. They are by definition shade tolerant. In large gaps, such as those created by fire or clearings, shade-tolerant seedlings often die and the replacement forest is of trees which germinate after the gap is created. These are called light demanding, pioneer (early successional) or secondary species. Unlike the shade tolerators (late successional), pioneers cannot regenerate under a canopy, not even their own, and depend for perpetuation on continually colonizing new large gaps. In large gaps, pre-existing shade tolerant seedlings are overtopped by vigorous-growing pioneers. The shade tolerant species which do not die as a result of competition, and persist suppressed in the shade of pioneers, eventually replace the short lived pioneers (see Whitmore 1975, 1982, 1983; Bazzaz and Pickett 1980, Bazzaz 1984).

It is now thought that different species have specific gap requirements but there is need for experimental evidence from various tropical ecosystems before a general trend can be made. Besides, the dichotomy of rainforest trees into two groups of species: light demanders (pioneer) and shade tolerators (climax) is too crude (Whitmore, 1983). Whitmore (1975) recognised four responses to gaps amongst just twelve common large tree species on Kolombangora Island:

- (i) species that establish and grow beneath closed canopies
- (ii) species that establish and grow beneath closed canopies but benefit from gaps
- (iii) species that establish under closed canopies but require gaps to mature and reproduce
- (iv) species that establish and reproduce only in gaps.

Thus, the process and pattern of secondary succession poses some major questions which need to be answered. E.g. does the tree flora of a given area contain secondary species, intermediate between pioneer and climax species ? Do species of all stages start simultaneously at the onset of gap formation or do they establish



sequentially with species later in succession developing below the pioneer canopy ? Whitmore (1983) and others do recognise that each species may be unique in its gap preference on a continuum.

It is not the intention of this discussion to go into details of secondary succession which involves population dynamics. Nevertheless, physiological responses as reported in the present work can be related to the ecological adaptation of species as observed in the natural environment. It is clear that ultimately, quantitative explanations of succession will require much detail of the species characteristics, such as those shown here for just a few species.

### 11.7 Management/silvicultural implications

Our present understanding of plant physiology and ecology has been gained from studies of temperate plants. When an equivalent amount of research has been done in the tropics, it will be necessary to re-approach the whole concept of present trial and error tropical moist forest management. For instance the concept of 'desirables' and 'undesirable' has led to selective creaming of these forests, and future demands of such wood will have to be met through forest plantations now in their infancy, or through some form of enrichment planting. The causes of poor natural regeneration and its control need further research to establish the factors involved such as vegetational shade-light and its influence on seed germination and seedling development. Thus, knowledge of species (physiological responses) in a given environment will enable us to construct models of succession and a basis of management that takes into account the whole forest instead of a few 'desirable' species. Moreover, it should ultimately be possible to predict the outcome of any attempt to divert succession in a desirable path, as in enrichment planting.

Appreciation of differences in species physiological responses in a particular forest location is an important silvicultural tool in forest management. Rational utilization to meet a given objective of management requires knowledge of factors limiting productivity such as moisture stress, temperature and nutrient availability. Shade has been



implicated as one of the main causes of poor natural regeneration. Natural regeneration is accounted for by the number of surviving seedlings and the number of seeds involved may be enormous. Physiological responses like those reported here, coupled with a knowledge of photon flux density and its spectral distribution, may enable controlled thinning to achieve regeneration. Possibly, mismanagement like that reported in section 1.4 may be averted. However, at present only a few studies have been carried out in this respect and control of natural regeneration remains one of the most serious constraints in understanding the reproduction of tropical forests.

In selectively logged forests, increasing the proportion of the so called desirable species such as during enrichment planting requires knowledge of species response to vegetational shade-light. In an attempt to make Budongo a mahogany forest, by opening up the canopy to increase the light levels reaching naturally regenerated and planted mahogany seedlings on the forest floor, resulted into further increase of pioneer (or weed) species. This would not have happened if growth responses to small and large canopy gaps were known at the time.

For some purposes, it is necessary to manage the forest to produce low density, fast growing, short lived pioneer species. A case like this would be averted if enrichment planting is carried out in large gaps and clearings. Fast growing pioneer species cannot withstand shade but can grow fast in the open; therefore can be utilized in large gaps where they encounter intraspecific competition, enhanced apical dominance and increased leaf area index to shade other species. These responses have been utilized in plantation monocultures: the lower most branches die continuously as a result of shading (self pruning) and trees develop relatively short narrow crowns. However, in un-even-aged mixed stands and natural forests, small seedlings and younger trees may grow slowly (depending on spacing density) and may be suppressed or overtopped by large, older and other fast growing trees. This fact is important in choice of species based on growth rates and other physiological attributes.



It is perhaps relatively unusual that physiological studies can be used directly in management. (This is even the case in agricultural sciences). More often they merely explain the underlying reason why a particular practice works. However, with the advent of tree breeding programmes including micropropagation and even genetic engineering; physiological studies may have an important role to play in the selection of genotypes to particular environments. Already Ladipo (1981) has shown that within one species there is an enormous variation in the photosynthetic response to light and in other parameters. Thus, within a species there appears to be scope for improvement.

Finally, it is important to attempt more research into the physiology and ecology of tropical moist forest species since there is a certain urgency for developing a framework for managing this vital but disappearing biosphere component. According to Myres (1980) "Tropical moist forests and their species stocks are being depleted more rapidly than some of the earth's most precious minerals". Evans (1976) warned that "mankind is like a lapidary with a sack of uncut diamonds. His resources are limited, he can only cut one at a time; to finish the sack would take a very long while. But meantime there are other ways of keeping warm than shooting the sackful into an anthracite stove and burning them up overnight". He called upon all individual ecologists to lose no opportunity of trying to convince the man with the sack that this is so; because conservation is preserving opportunities for the future.



APPENDIX A1: ANALYSIS OF VARIANCE

VARIATE:  $g_s$

Source of Variation Experimental Factors	Degrees of Freedom	Sum of Squares	Sum of Squares (%)	Mean Squares	Variance ratio (F)	Level of Significance P<
Photon Flux Density (PFD)	6	1.0786266	71.28	0.1797711	208.543	0.001
Light Regime during growth	1	0.1219658	8.06	0.1219658	141.486	0.001
Species	3	0.0049142	0.32	0.0016381	1.900	n.s.
PFD.Light	6	0.0246482	1.63	0.0041080	4.766	0.001
PFD.Species	18	0.0389830	2.58	0.0021657	2.512	0.001
Light.Species	3	0.0253196	1.67	0.0084399	9.791	0.001
PFD.Light.species	18	0.0255817	1.69	0.0014212	1.649	0.05
Residual	224	0.1930957	12.76	0.0008620		
TOTAL	279	1.5131311	100.00	0.0054234		
GRAND TOTAL	279	1.5131311	100.00			
GRAND MEAN	0.1289	{ $\text{mol m}^{-2} \text{ s}^{-1}$ }				
TOTAL NUMBER OF OBSERVATIONS	280					

N.S. = Not significant at  $P < 0.05$

APPENDIX TABLE 1: Stomatal conductance data for the four tree species grown at either low or high photon flux density were pooled in order to investigate species differences. From the above, the species did not significantly differ in their stomatal conductance (see Fig.9.1).  
Logarithmic transformation of the same data is shown in Appendix Table A4.

F 0.001 (1,224) = 10.83, F 0.001 (3,224) = 5.42, F 0.001 (6,224) = 3.74, F 0.001 (18,224) = 2.36  
F 0.05 (1,224) = 3.84, F 0.05 (3,224) = 2.60, F 0.05 (6,224) = 2.10, F 0.05 (18,224) = 1.61



APPENDIX A2: ANALYSIS OF VARIANCE

VARIATE: ASSIMILATION RATE (on a leaf area basis)

Source of Variation Experimental Factors	Degrees of Freedom	Sum of Squares	Sum of Squares (%)	Mean Squares	Variance ratio (F)	Level of Significance p<
Photon Flux Density During Measurements (PFD)	6	1391.1313	68.04	231.8552	353.005	0.001
Light Regime During Growth (light)	1	118.4654	5.79	118.4654	180.366	0.001
Species	3	90.8159	4.44	30.2720	46.090	0.001
PFD.Light	6	172.2827	8.43	28.7138	43.717	0.001
PFD.Species	18	45.8300	2.24	2.5461	3.877	0.001
Light.Species	3	49.5313	2.42	16.5104	25.138	0.001
PFD.Light.Species	18	29.3259	1.43	1.6292	2.481	0.001
Residual	224	147.1241	7.20	0.6568		
TOTAL	279	2044.5059	100.00	7.3280		
GRAND TOTAL	279	2044.5059	100.00			
GRAND MEAN						
TOTAL NUMBER OF OBSERVATIONS		3.110 (μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	280			

APPENDIX TABLE 2: Photosynthesis data for the four tree species grown at either low or high photon flux density were pooled to investigate species performance. All the above experimental factors had significant effects on the rate of photosynthesis (see Figs. 9.2, 9.3 and 9.4 a-d).



## APPENDIX A3: ANALYSIS OF VARIANCE

VARIATE: ASSIMILATION RATE (On a dry weight basis)

Source of Variation Experimental Factors	Degrees of Freedom	Sum of Squares	Sum of Squares	Sum of Squares (%)	Variable ratio (F)	Level of Significance $p <$
Photon Flux Density During Measmts (PFD)	6	0.4845291	56.99	0.0807548	339.811	0.001
Light Regime During Growth (Light)	1	0.0479684	5.64	0.0479684	201.848	0.001
Species	3	0.1473183	17.33	0.0491061	206.635	0.001
PFD.Light	6	0.0203674	2.40	0.0033946	14.284	0.001
PFD.Species	18	0.0600293	7.06	0.0033350	14.033	0.001
Light.Species	3	0.0242551	2.85	0.0080850	34.021	0.001
PFD.Light.Species	18	0.0124635	1.47	0.0006924	2.914	0.001
Residual	224	0.0532328	6.26	0.0002376		
TOTAL	279	0.8501636	100.00	0.0030472		
GRAND TOTAL	279	0.8501636	100.00			
GRAND MEAN		0.06156 ( $\mu\text{mol g}^{-1} \text{s}^{-1}$ )				
TOTAL NUMBER OF OBSERVATIONS	280					

APPENDIX TABLE 3: Analysis of variance of experimental factors, re-expressed on a dry weight basis (see Figs. 9.5 and 9.6).



APPENDIX A4: LOG TRANSFORMATION

ANALYSIS OF VARIANCE

VARIATE :  $g_s$

Source of Variation  
Experimental Factors

Photon Flux Density During Msmts. (PFD)  
Light Regime During Growth (Light)  
Species  
PFD.Light  
PFD.Species  
Light.Species  
PFD.Light.Species  
Residual  
TOTAL

Degree of Freedom	Sum of Squares	Sum of Squares (%)	Mean Squares	Variance ratio (F)	Level of Significance P<
6	119.54556	75.68	19.92426	275.990	0.001
1	9.59753	6.08	9.59753	132.945	0.001
3	0.44356	0.28	0.14785	2.048	n.s.
6	2.03611	1.29	0.33935	4.701	0.001
18	2.44238	1.55	0.13589	1.880	0.05
3	3.87623	2.45	1.29208	17.898	0.001
18	3.85533	2.44	0.21429	2.967	0.001
224	16.17096	10.24	0.07229		
279	157.96762	100.00	0.56629		
279	157.96762	100.00			

GRAND TOTAL

GRAND MEAN

TOTAL NUMBER OF OBSERVATIONS

-2.269  
280

APPENDIX TABLE A4: Logarithmic transformation of stomatal conductance data was carried out. As shown, logarithmic transformation only affected the level of significance but not the results that have been declared significant (compare with Appendix A1).



## APPENDIX A5: ANALYSIS OF VARIANCE

VARIATE:  $g_s$ 

Source of Variation Experimental Factors	Degrees of	Sum of squares	Sum of squares (%)	Mean squares	Variance ratio (F)	Level of significance P <
Photon Flux Density During Measmts (PPFD)	6	0.203900	46.92	0.033983	18.694	0.001
Red/Far-Red Ratio during growth (R/FR)	1	0.002433	0.56	0.002433	1.338	n.s.
Species	1	0.004281	0.99	0.004281	2.355	n.s.
PPFD.RFR	6	0.005256	1.21	0.000876	0.482	n.s.
PPFD.Species	6	0.002393	0.55	0.000399	0.219	n.s.
RFR.Species	1	0.007787	1.79	0.007787	4.283	0.05
PPFD.RFR.Species	6	0.004914	1.13	0.000819	0.451	n.s.
Residual	112	0.203605	46.85	0.001818		
TOTAL	139	0.434569	100.00	0.003126		
GRAND TOTAL	139	0.434569	100.00			
GRAND MEAN	0.1010					
TOTAL NUMBER OF OBSERVATIONS	140					

F 0.001 (6,112) = 4.08, F 0.001 (1,112) = 11.45, F 0.05 (6,112) = 1.82, F 0.05 (1,112) = 3.93

APPENDIX TABLE A5: Analysis of variance for stomatal conductance to water vapour ( $g_s$ ) as reported in Chapter 10. Data for *Terminalia ivorensis* and *Khaya senegalensis* grown at  $125 \mu\text{mol m}^{-2} \text{s}^{-1}$  were pooled to investigate the general effect of RFR ratio on stomatal conductance.



## APPENDIX A6: ANALYSIS OF VARIANCE

VARIATE: Assimilation rate (on a leaf area basis)						
Source of Variation Experimental Factor	Degrees of Freedom	Sum of Squares	Sum of Squares (%)	Mean Squares	Variance ratio (F)	Level of Significance P <
Photon Flux Density (PPFD)	6	498.3538	81.35	83.0590	149.841	0.001
Red/Far-red ratio during growth	1	28.0015	4.57	28.0015	50.516	0.001
Species	1	1.4954	0.24	1.4954	2.698	N.S.
PPFD.RFR	6	16.1447	2.64	2.6908	4.854	0.001
PPFD.Species	6	1.0830	0.18	0.1805	0.326	N.S.
RFR.Species	1	0.0000	0.00	0.0000	0.000	N.S.
PPFD.RFR.Species	6	5.4522	0.89	0.9087	1.639	N.S.
Residual	112	62.0833	10.13	0.5543		
TOTAL	139	612.6135	100.00	4.4073		
GRAND TOTAL	139	612.6135	100.00			
GRAND MEAN		2.755 ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )				
TOTAL NUMBER OF OBSERVATIONS		140				

Appendix Table A6: The effect of R/FR ratio on the rate of photosynthesis. Data for both *Terminalia ivorensis* and *Khaya senegalensis* were pooled to investigate the influence of R/FR during growth at low photon flux density as described in Chapter 10 (refer to Figs 10.1 and 10.2).



APPENDIX A7: ANALYSIS OF VARIANCE

VARIATE: ASSIMILATION RATE (expressed on a dry weight basis)

Source of Variation Experimental Factors	Degrees of Freedom	Sum of Squares	Sum of Squares (%)	Mean Squares	Variance Ratio (%)	Level of Significance P<
Photon Flux Density During Msmts (PFD)	6	0.2723050	62.27	0.0453842	141.410	0.001
Red/Far-Red Ratio During Growth (RFR)	1	0.0542614	12.41	0.0542614	169.070	0.001
Species	1	0.0296698	6.78	0.0296698	92.447	0.001
PFD.RFR	6	0.0240395	5.50	0.0040066	12.484	0.001
PFD.Species	6	0.0159540	3.65	0.0026590	8.285	0.001
RFR.Species	1	0.0040651	0.93	0.0040651	12.666	0.001
PFD.RFR.Species	6	0.0010763	0.25	0.0001794	0.559	n.s.
Residual	112	0.0359452	8.22	0.0003209		
TOTAL	139	0.4373159	100.00	0.0031462		

GRAND TOTAL

GRAND MEAN

TOTAL NUMBER OF OBSERVATIONS

0.0642 ( $\mu\text{mol g}^{-1} \text{s}^{-1}$ )  
140

APPENDIX TABLE A7: The effect of R/FR ratio on the rate of photosynthesis (re-expressed on a dry weight basis)  
Data for both *Terminalia ivorensis* and *Khaya senegalensis* were pooled (refer to Figs. 10.3 -10.5).  
Msmts = measurements



## REFERENCES

- AGEEVA, O.G. (1977). Effects of light on thermostability of Hill reaction in pea and spinach chloroplast. *Photosynthetica* 11: 1-4.
- ALLEE, W.C. (1926). Measurement of environmental factors in the tropical rainforest of Panama. *Ecology* 7: 273-302.
- ALUMA, R.J.W. (1979). Uganda: a damage report. *Unasyiva* 31(126): 20-24.
- ALVEY, N., GALWEY, N. and LANE, P. (1982). *An Introduction to GENSTAT*. Academic Press, London, New York, Paris, San Diego, San Francisco, Sao Paulo, Sydney, Tokyo and Toronto.
- AMPOFO, S.T. and LAWSON, G.W. (1972). Growth of seedlings of *Afrormosia elata* harms in relation to light intensity. *J. Appl. Ecol.* 9: 301-306.
- ANDERSON, M.C. (1966). Some problems of simple characterization of light climate in plant communities. In *Light as an Ecological Factor* (Eds. R. Bainbridge, G. C. Evans and O. Rackman) pp. 77-90. Blackwell, Oxford.
- ANDERSON, J.M., GOODCHILD, D.J. and BOARDMAN, N.K. (1973). Composition of the photosystems and chloroplast structure in extreme shade plants. *Biochem. Biophys. Acta* 325: 573-585.
- BAUR, G.N. (1964). Rainforest treatment. *Unasyiva* 18: 18-28.
- BAZZAZ, F.A. (1979). The physiological ecology of plant succession. *Ann. Rev. Ecol. Syst.* 10: 351-371.
- BAZZAZ, F.A. (1984). Dynamics of wet tropical forests and their species strategies. In *Physiological Ecology of Plants of the Wet Tropics* (Eds: E. Medina, H.A. Mooney, and C. Vázquez-Yanes). *Tasks for Vegetation Science* 12: 233-243. Dr. W. Junk, The Hague, Boston, Lancaster.
- BAZZAZ, F.A. and CARLSON, R.W. (1982). Photosynthetic acclimation to variability in the light environment of early and late successional plants. *Oecologia* 54: 313-316.
- BAZZAZ, F.A. and PICKETT, S.T.A. (1980). Physiological ecology of tropical succession: A comparative review. *Ann. Rev. Ecol. Syst.* 11: 287-310.
- BEARDSSELL, M.F., JARVIS, P.G. and DAVIDSON, B. (1972). A null-balance diffusion porometer suitable for use with leaves of many shapes. *J. Appl. Ecol.* 9: 677-690.



- BERNARD-REVERSAT (1978). ORSTOM. In Tropical Forest Ecosystems, Natural Resources Research. XIV: State of Knowledge. UNESCO/UNEP/FAO.
- BINGHAM, G.E. and COYNE, P.J. (1971). A portable, temperature-controlled, steady-state porometer for field measurement of transpiration and photosynthesis. *Photosynthetica* 11(1): 148-160.
- BJÖRKMAN, O. (1968). Carboxydismutase activity in shade-adapted and sun-adapted species of higher plants. *Physiol. Plant.* 21: 1-10.
- BJÖRKMAN, O. (1968b). Further studies on differentiation of photosynthetic properties of sun and shade ecotypes of *Solidago virgaurea*. *Physiol. Plant.* 21: 84-99.
- BJÖRKMAN, O. (1973). Comparative studies on photosynthesis in higher plants. Carn. Inst. Washington. Publication No. 492. pp. 1-63.
- BJÖRKMAN, O. (1981). Responses to different quantum flux densities. In *Encyclopedia of Plant Physiology, Physiological Plant Ecology* (Eds. O.L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler) 12A: 57-107.
- BJÖRKMAN, O., BOARDMAN, N.K., ANDERSON, J.M., THORNE, S.W., GOODCHILD, D. J. and PYLIOTIS, N.A. (1972). Effects of light intensity during growth of *Atriplex patula* on the capacity of photosynthetic reactions, chloroplast components and structure. *Carn. Inst. Washington Year Book* 71: 115-135.
- BJÖRKMAN, O. and HOLMGREN, P. (1963). Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. *Physiol. Plant.* 16: 889-914.
- BJÖRKMAN, O. and HOLMGREN, P. (1966). Photosynthetic adaptation to light intensity in plants native to shaded and exposed ecotypes. *Physiol. Plant.* 19: 854-859.
- BJÖRKMAN, O. and LUDLOW, M.M. (1972). Characterization of light climate on the forest floor of a Queensland rainforest. *Carn. Inst. Washington YearBook* 71: 85-94.
- BJÖRKMAN, O. and POWLES, S.B. (1981). Leaf movement in shade species *Oxalis oregana*. 1. Response to light levels and light quality. *Carn. Inst. Washington Year Book* 80: 59-62.
- BLACK, M. (1979). Light-controlled germination of seeds. In *Dormancy and survival. Symposium of the Society for Experimental Botany.* No. XXIII. pp. 193-217. Cambridge University Press.



- BLACKMAN, G. E. (1968). The application of the concepts of growth analysis to the assessment of productivity. In : Functioning of Terrestrial Ecosystems at the Primary Production Level (Proceedings of the Copenhagen Symposium). Ed. F.E.Eckardt, pp. 243-259. UNESCO, Paris.
- BLACKMAN, G.E. and WILSON, G.L. (1951). Physiological and ecological studies in the analysis of plant environment. VII. An analysis of the different effects of light intensity on the net assimilation rate, leaf area ratio and relative growth rate of different species. *Ann. Bot.* 15: 373-408.
- BMDP, PAR. Derivative-free non-linear regression package. In: BMDP statistical software 1981. Department of Biomathematics, University of California.
- BOARDMAN, N.K. (1977). Comparative photosynthesis of sun and shade plants. *Ann. Rev. Plant Physiol.* 28: 355-377.
- BODOWSKI, G. (1980). The place of Agro-Forestry in managing Tropical forests. In: Tropical Forests : Utilization and Conservation. Ed. F. Mergen, pp. 181-194. Proceedings of an International Symposium held at Yale School of Forestry (April 15-16, 1980). New Haven, CT, U.S.A.
- BOGORAD, P.C. and McILATH, W.J. (1960). Effect of light quality on axillary bud development in *Xanthium*. *Plant Physiol.* 35: Suppl. 32.
- BORTHWICK, H.A., HENDRICKS, S.B., PARKER, M.W., TOOLE, E.H. and TOOLE, V.K. (1952). A reversible photoreaction controlling seed germination. *Proc. Nat. Acad. Sci. USA.* 38: 662-666.
- BOURDEAU, P.F. (1959). Seasonal variation of photosynthetic efficiency of evergreen conifers. *Ecology* 40: 63-67.
- BOURDEAU, P.F. and LAVERICK, M.L. (1958). Tolerance and photosynthetic adaptability to light intensity in white pine, red pine and *Ailanthus* seedlings. *For. Sci.* 4: 196-207.
- BRIGGS, W.R. (1981). Annual Report of the Director Department of Plant Physiology, Carnegie Institution. Carn. Inst. Washington Year Book 80: 7-15.
- BROWN, W.H. (1919). Vegetation of Phillipine Mountains. *Publs. Bur. Sci. Govt. Labs, Manila*, No. 13.
- BRÜNIG, E. (1947). In den Waldern Nordsumatras, Bonn. F. Dummlers.
- BRÜNIG, E.F. (1977). The Tropical rain forest - A wasted asset or an



- essential biospheric resource ? *Ambio.* 6(4): 187-191.
- CACHAN, P. (1963). Signification ecologique des variations microclimatiques verticales dans la foret sempervirente de basse cote d'Ivoire. *Ann. Fac. Sci. Dakar* 8: 89-155.
- CARTER, G.S. (1934). Reports of the Cambridge Expedition to British Guiana, 1933. Illumination in the rain forest at ground level. *J. Linn. Soc. (Zool.)* 38: 579-589.
- di CASTRI, F., HARDLEY, M. and DAMLAMIAN, J. (1981). The Man and the Biosphere program as an evolving system. *Ambio.* 10 (2-3): 52-57.
- CATINOT, R. (1970). Results of enrichment planting in the Tropics. FAO Committee on Forest Development in the Tropics. Rome, October 1969. FAO:FDT-69/4: 38-43.
- CAUFIELD, C. (1982). Tropical Moist Forests. Earthscan, London.
- CHARTIER, P., MOROT-GAUDRY, J.F., BETHENOD, O. and THOMAS, D.A. (1977). The net assimilation of  $C_3$  and  $C_4$  plants as influenced by light and carbon dioxide, and analysis of the role of the Gene Opaque 2 in young maize. In: Environmental Effects on Crop Physiology (Eds. J.J. Landsberg and C. V. Cutting). pp. 125-136. Academic Press, London, New York and San Francisco.
- COLLINS, W.B. (1966). Floral initiation in strawberry and some effects of red-far irradiation as components of continuous white light. *Can. J. Bot.* 44: 663-668.
- COOMBE, D.E. (1957). The spectral distribution of shadelight in woodlands. *J. Ecol.* 45: 823-830.
- COOMBE, D.E. (1960). An analysis of the growth of *Trema guineensis*. *J. Ecol.* 48: 219-231.
- COOMBE, D.E. and HADFIELD, W. (1962). An analysis of the growth of *Musanga cecropioides*. *J. Ecol.* 50(1): 221-234.
- COOMBS, J. and HALL, D.O. (1980). Techniques in Bioproductivity and Photosynthesis. Pergamon Press, London.
- CORNER, E. J. H. (1954). The evolution of tropical forest. In Evolution as a process (Eds. J. S. Huxley, A. C. Hardy and E. B. Ford), pp. 34-46. Allen and Unwin, London.
- CORRÉ, W. J. (1983a). Growth and morphogenesis of sun and shade plants. 1. The influence of light intensity. *Acta Bot. Neerl.* 32(1 ): 49-62.
- CORRÉ, W.J. (1983b). Growth and morphogenesis of sun and shade plants.



- II. The influence of light quality. *Acta Bot. Neerl.* 32(3): 185-202.
- CORRÉ, W.J. (1983c). Growth and morphogenesis of sun and shade plants. III. Combined effects of light intensity and nutrient supply. *Acta Bot. Neerl.* 32(4): 277-294.
- CRAWFORD, R.M.M. (1982). Physiological responses to flooding. In: *Physiological Plant Ecology II (Water Relations and Carbon Assimilation)*, [Eds. O.L. Lange, P.S. Nobel, C. B. Osmond and H. Ziegler] 12B: 453-477. Springer-Verlag, Berlin, Heidelberg, New York.
- CROOKSTON, R.K., TREHARNE, K.J., LUDFORD, P. and OZBUN, J.L. (1975). Response of beans to shading. *Crop Sci.* 15(3): 412-416.
- DAWKINS, H.C. (1958). The management of natural tropical high forest with special reference to Uganda. *Imp. For. Inst. Paper No.* 34.
- DENNY, P. (1973). Lakes of South-Western Uganda. II. Vegetation studies of Lake Bunyonyi. *Freshwater Biology* 3: 123-135.
- DENSLow, J.S. (1978). Mechanisms of succession in a tropical rainforest - a contribution from Mexico. *Ecology* 59:862.
- DIETZER, G.F., HAYES, R. and JABBEN, M. (1979). Kinetics and time dependence of the effects of far-red light on the photo-periodic induction of flowering in Wintex barley. *Plant Physiol.* 64: 1015-1021.
- van DOBBEN, W.H., van AST, A. and CORRÉ, W.J. (1981). The influence of light intensity on morphology and growth rate of bean seedlings. *Acta. Bot. Neerl.* 30: 33-45.
- DOSSO, H., GUILLAUMET, J.L. and HADLEY, M. (1981). Tai project : Land use problems in a tropical rainforest. *Ambio.* 10(2-3): 120-125.
- DOWNS, R.J., HENDRICKS, S.B. and BORTHWICK, H. A. (1957). Photoreversible control of elongation in Pinto beans and other plants under normal conditions of growth. *Bot. Gaz.* 118: 199-208.
- DOWNTON, W.J.S. (1975). The occurrence of  $C_4$  photosynthesis among plants. *Photosynthetica* 9: 96-105.
- DUNCAN, W.G., LOOMIS, R.S., WILLIAMS, W.A. and HANAU, R. (1967). A Model for Simulating Photosynthesis in Plant Communities. *Hilgardia.* 38(4): 181-205.



- EDMISTON, J. (1970). Some autecological studies of *Ormosia krugii*. In: A tropical rain forest. A study of irradiation and ecology at El verdi, Puerto Rico. (Eds. E. D. Odum and R. F. Pigeon). Vol. 1, pp. B291-B298. Office Inform. Serv., U.S. Atomic Energy Commission, Washington.
- EGGELING, W.J. (1940). Budongo forest. Emp. For. J. 19: 179-196.
- EGGELING, W.J. (1947). Working plan for the Budongo and Siba Forests. First revision period 1945-1954. Forestry Department, Uganda Government Printer.
- ELIÁS, P. (1979). Some ecophysiological features in leaves of plants in an oak-hornbeam forest. Phytotax. 14: 29-42.
- EREZ, A. (1977). The effect of different portions of sunlight spectrum on ethylene evolution in peach (*Prunus persica*) apices. Physiol. Plant. 39: 285-289.
- EVANS, G.C. (1939). Ecological studies on the rain forest of Southern Nigeria. II. The atmospheric environmental conditions. J. Ecol. 27: 436-482.
- EVANS, G. C. (1956). An area survey method of investigating the distribution of light intensity in woodlands, with particular reference to sunflecks. J. Ecol. 44: 391-428.
- EVANS, G.C. (1972). The Quantitative Analysis of Plant Growth. Blackwell, Oxford.
- EVANS, G.C. (1976). A sack of uncut diamonds: the study of ecosystems and the future resources of mankind. J. Ecol. 64: 1-39.
- EVANS, J. (1982). Plantation Forestry in the Tropics. Clarendon Press, Oxford.
- EVANS, G. C. and HUGHES, A.P. (1961). Plant growth and the aerial environment. I. Effects of artificial shading on *Impatiens parviflora*. New Phytol. 60: 150-180.
- EVANS, G.C., WHITMORE, T.C. and WONG, Y.K. (1960). The distribution of light reaching the ground vegetation in a tropical rain forest. J. Ecol. 48: 193-204.
- FARQUHAR, G.D., von CAEMMERER, S. and BERRY, J.A. (1980). A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species. Planta 149: 78-90.
- FARQUHAR, G.D. and SHARKEY, T.D. (1982). Stomatal conductance and photosynthesis. Ann. Rev. Plant Physiol. 33: 317-345.



- FASEHUN, F.E. and AUDU, M. (1980). Comparative seedling growth and respiration of four tropical hardwood species. *Photosynthetica* 14(2): 193-197.
- FEDERER, C.A. and TANNER, C. B. (1966). Spectral distribution of light in the forest. *Ecology* 47: 555-560.
- FETCHER, N., STRAIN, B.R. and OBERBAUER, F. (1983). Effects of light regime on the growth, leaf morphology, and water relations of seedlings of two species of tropical trees. *Oecologia* 58: 314-319.
- FIELD, C. and MOONEY, H.A. (1984). Measuring of gas exchange of plants in the wet tropics. In: *Physiological ecology of plants of the wet tropics. Tasks for vegetation science 12* (Eds. E. Medina, H. A. Mooney and C. Vazquez-Yanes), pp. 129-138. Dr. W. Junk publishers. The Hague, Boston, Lancaster.
- FISHER, R.A. (1921). Some remarks on the methods formulated in a recent article on 'The quantitative analysis of plant growth'. *Ann. Appl. Biol.* 7: 367-372.
- FITTER, A.H. and ASHMORE, C.J. (1974). Response of two *Veronica* species to a simulated woodland light climate. *New Phytol* 73: 997-1001.
- FITTER, A. H. and HAY, R. K. (1981). *Environmental Physiology of Plants*. Academic Press, London, New York, Toronto, Sydney and San Francisco.
- FOX, J. E. D. (1968). Exploitation of the Gola Forest. *J. W. Afri. Sci. Ass.* 13(2): 185-210.
- FRANKLAND, B. and LUTENDRE, R. J. (1978). Phytochrome and effects of shading on growth of woodland plants. *Photochem. Photobiol.* 27: 223-230.
- FREDERICQ, H. and De GREEF, J.A. (1966). Red, far-red photoreversible control of growth and chlorophyll content in light growth thalli of *Marchantia polymorpha* L. *Naturwissenschaften* 53: 337-341.
- FRIEND, D. J. C., HELSON, V. A., and FISCHER, J.E. (1961). The influence of the ratio of incandescent to fluorescent light on the flowering response of Marquis wheat grown under controlled conditions. *Can. J. Plant Sci.* 41: 418-427.
- GAASTRA, P. (1959). Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature and stomatal diffusion resistance. *Mededelingen van de Land Landbouwhoogeschool te Wageningen*, 59: 1-68.



- GABRIELSEN, E.K. (1948). Effects of different chlorophyll concentrations on photosynthesis in foliage leaves. *Physiol. Plant.* 1: 5-37.
- GAUDET, J.J. (1975). Mineral concentrations in papyrus in various African swamps. *J. Appl. Ecol.* 63: 483-491.
- GAUDET, J.J. (1977). Natural drawdown on Lake Naivasha, Kenya, and the formation of papyrus swamps. *Aquatic Botany* 3: 1-47.
- GAUHL, E. (1969). Differential photosynthetic performance of *Solanum dulcamara* ecotypes from shaded and exposed habitats. *Carn. Inst. Washington Year Book* 67: 482-488.
- GAUHL, E. (1970). Leaf factors affecting the rate of light saturated photosynthesis in ecotypes of *Solanum dulcamara*. *Carn. Inst. Washington Year Book* 68: 633-636.
- GAUHL, E. (1976). Photosynthetic response to varying light intensity in ecotypes of *Solanum dulcamara* L. from shaded and exposed habitats. *Oecologia* 22: 275-286.
- GÓMEZ-POMPA, A. and VÁZQUEZ-YÁNES, C. (1974). Studies on the secondary succession in tropical lowlands. In: *Proceedings of the First International Congress of Ecology*. The Hague, The Netherlands pp. 336-342.
- GÓMEZ-POMPA, A., VÁZQUEZ-YÁNES, C. and GUEVFRA, C. (1972). The tropical rain forest: A non-renewable resource. *Science* 177: 762-765.
- GOODCHILD, D.J., BJÖRKMAN, O. and PYLIOTIS, N.A. (1972). Chloroplast ultrastructure, leaf anatomy, and content of chlorophyll and soluble protein in rainforest species. *Carn. Inst. Washington Year Book* 71: 102-107.
- GOUDRIAAN, J. (1978). A family of saturation type curves, especially in relation to photosynthesis. *Ann. Bot.* 43: 783-785.
- GRACE, J., FASEHUN, F.E. and DIXON, M. (1980). Boundary layer conductance of some tropical timber trees. *Plant Cell and Environment* 3: 443-450.
- GRACE, J., OKAI, D.U.U. and FASEHUN, F.E. (1982). Stomatal conductance of two tropical trees during the wet season in Nigeria. *J. Appl. Ecol.* 19: 659-670.
- GRAINGER, A. (1980). The state of the World's Tropical Forests. *The Ecologist* 10(1<sub>2</sub>): 1-54.
- De GREEF, J.A. and FREDERICQ, H. (1972). Enhancement of senescence by far-red light. *Planta* 104: 272-274.



- GREGORY, R.P.F. (1977). *Biochemistry of Photosynthesis*. John Wiley, London, New York, Sydney, Toronto.
- GREON, J. (1973). Photosynthesis of *Calendula officinalis* L. and *Impatiens parviflora* DC., as influenced by light intensity during growth and age of leaves and plants. *Meded. Landbouwhogeschool Wageningen* 73(8): 1-128.
- GRIBBIN, J. (1979). *Climate and Mankind*. Earthscan, London.
- GRIFFITHS, J.H. (1983). Field investigations of CO<sub>2</sub> uptake in Sitka spruce. M. Phil. Thesis, University of Edinburgh.
- GRIFFITHS, J.H. and JARVIS, P.G. (1981). A null balance carbon dioxide and water vapour porometer. *J. Expt. Bot.* 32(131): 1157-1168.
- GRIME, J. P. (1965). Shade tolerance in flowering plants. *Nature* 208: 161-163.
- GRIME, J. P. (1966). Shade avoidance and shade tolerance in flowering plants. In: *Light as an ecological factor* (eds. R. Bainbridge, G. C. Evans and O. Rackham). Blackwell, Oxford pp. 187-207.
- GRIME, J.P. (1977). Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111: 1169-1194.
- HADFIELD, W. (1974). Shade in North-East Indian tea plantations. II. Foliar illumination and canopy characteristics. *J. Appl. Ecol.* 11: 179-199.
- HALL, A.E. (1979). A model of leaf photosynthesis and respiration for predicting carbon dioxide assimilation in different environments. *Oecologia* 143: 299-316.
- HARRISON, J.L. (1968). The effect of forest clearance on small mammals. *Unasylva* 28: 127-143.
- HEATHCOTE, L., BAMBRIDGE, K.R. and McLAREN, J.S. (1979). Specially constructed growth cabinets for simulation of the spectral photon distributions found under natural vegetation canopies. *J. Expt. Bot.* 30: 347-353.
- HEPPER, N. (1978). Growing your own paper: History and cultivation of *Cyperus papyrus*. *Greenhouse* 2(7): 47, 49-50.
- HERERA, R., JORDAN, C.F., MEDINA, E., and KLINGE, H. (1981). How human activities disturb the nutrient cycles of a tropical rainforest in Amazonia. *Ambio*. 10(2-3): 109-114.
- HOCK, B. and MOHR, B. (1964). Die Regulation der O<sub>2</sub>-Aufnahme von



- Senfkemlingen *Sinapsis alba* L. durch licht. *Planta* 61: 209-228.
- HODDINOTT, J. and BAIN, J. (1979). The influence of simulated canopy light on the growth of six apocarpous moss species. *Can. J. Bot.* 57: 1236-1242.
- HOLMES, M.G. and SMITH, H. (1975). The function of phytochrome in plants growing in the natural environment. *Nature* 254: 512-514.
- HOLMES, M.G. and SMITH, H. (1977). The function of phytochrome in the natural environment. I. Characterization of daylight for studies in photomorphogenesis and photoperiodism. *Photochem. Photobiol.* 25: 533-538.
- HOLMES, M.G. and SMITH, H. (1977b). The function of phytochrome in natural environment. II. The influence of vegetation canopies on the spectral energy distribution of natural daylight. *Photochem. Photobiol.* 25: 539-546.
- HOLMES, M.G. and SMITH, H. (1977c). The function of phytochrome in the natural environment. IV. Light quality and plant development. *Photochem. Photobiol.* 25: 551-557.
- HOLMGREN, P., JARVIS, P.G. and JARVIS, M.S. (1965). Resistance to carbon dioxide and water vapour transfer in leaves of different plant species. *Physiol. Plant.* 18: 557-573.
- HOROI, T. and MONSI, M. (1963). Physiological and ecological analysis of shade tolerance of plants. 3. Effects of shading on growth attributes of *Helianthus annuus*. *Bot. Mag. (Tokyo)* 76: 121-129.
- HOWLAND, P. and BOWEN, M.R. (1977). *Triplochiton scleroxylon* K. schum. and other West African tropical hardwoods. West African Hardwoods Improvement Project, Research Report 1971-1977, Forestry Research Institute of Nigeria.
- HUGUET, I. (1983). Replenishing the World's forests: The future of the World's tropical forests. *Comm. For. Rev.* 62(3): 195-200.
- HUNT, R. (1978). *Plant Growth Analysis. Studies in Biology* No. 96. Edward Arnold, London.
- HUNT, R. (1982). *Plant Growth Curves. The functional approach to growth analysis.* Edward Arnold, London.
- HURD, R.G. (1974). The effect of an incandescent supplement on the growth of tomato plants in low light. *Ann. Bot.* 38: 613-623.
- HUTCHINSON, T. C. (1967). Comparative studies of the ability of species to withstand prolonged periods of darkness. *J. Ecol.* 55:



291-299.

- HUXLEY, P. (1967). The effects of artificial shading on some growth characteristics of Arabica and Robusta coffee seedlings. I. The effects of shading on dry weight, leaf area and derived growth data. *J. Appl. Ecol.* 4: 291-308.
- IRVINE, F.R. (1961). *Woody Plants of Ghana with special reference to their uses.* Oxford University Press, London.
- JACKSON, P. (1983). The tragedy of our tropical rainforests. *Ambio* 12(5): 252-254.
- JARVIS, P.G. (1971). The estimation of resistances to carbon dioxide transfer. In: *Plant Photosynthetic Production : Manual of Methods.* (Eds. Z. Šesták, J. Catský and P.G. Jarvis), pp. 566-631. Dr. W. Junk, The Hague.
- JARVIS, P.G. (1980). Stomatal response to water stress in conifers. In: *Adaptation of Plants to Water and High Temperature Stress* (Eds. N.C. Turner and P. J. Kramer), pp. 105-122. Wiley-Interscience, New York.
- JARVIS, P.G. (1981). Stomatal conductance, gas exchange and transpiration. In *Plants and their Atmospheric Environment* (Eds. J. Grace, E. D. Ford and P. G. Jarvis), pp. 175-204. Blackwell, Oxford.
- JARVIS, P.G. and ČATSKÝ, J. (1971). General principles of gasometric methods and the main aspects of installation design. In: *Plant Photosynthetic Production: Manuals of Methods* (Eds. Z. Sestak, J. Catsky and P. G. Jarvis), pp. 49-77. Dr. W. Junk, The Hague.
- JARVIS, P.G. and JARVIS, M.S. (1964). Growth rates of woody plants. *Physiol. Plant.* 17: 654-666.
- JARVIS, P.G. and MORISON, J.I.L. (1981). The control of transpiration and photosynthesis by the stomata. In. *Stomatal Physiology* (Eds. P.G. Jarvis and T.A. Mansfield), pp. 248-279. S.E.B. Seminar Series No. 8, Cambridge University Press, London, New York, New Rochelle, Melbourne, Sydney.
- JOHNSON, N.E. (1976). Biological opportunities and risks associated with fast growing plantations in the tropics. *Journal of Forestry* 74(4): 206-211.
- JONES, A.P.D. (1948). *The Natural Forest Inviolable Plot.* Nigerian



Forestry Department.

- JONES, B.M. and MILBURN, R.T. (1978). Photosynthesis in papyrus (*Cyperus papyrus* L.). *Photosynthetica* 12: 197-199.
- JONES, E.W. (1955). Ecological studies on the rainforest of Southern Nigeria. IV. The Plateau Forest of the Okumu Forest Reserve. *J. Ecol.* 43: 564-594.
- JONES, E.W. (1956). Ecological studies on the rainforest of Southern Nigeria. IV. The Plateau Forest of the Okumu Forest Reserve. (Contd.). *J. Ecol.* 44: 83-117.
- JONES, H.G. (1983). *Plants and Microclimate. A quantitative approach to environmental plant physiology.* Cambridge University Press, London, New York, New Rochelle, Melbourne, Sydney.
- JONES, M. (1983a). Papyrus: a new fuel for the Third World. *New Scientist* 99(1370): 418-421.
- KANEMASU, E.T., THURTELL, G.W. and TANNER, C.B. (1969). Design, calibration and field use of a stomatal diffusion porometer. *Plant Physiol.* 44: 881-885.
- KARTAWINATA, K., ADISOEMARTO, S., RISWAN, S. and VAYDA, A. (1981). The impact of man on a tropical forest in Indonesia. *Ambio* 10(2-3): 115-119.
- KASPERBAUER, M.J. (1971). Spectral distribution of light in a tobacco canopy and effects of end-of-day light quality on growth and development. *Plant Physiol.* 47: 775-778.
- KASPERBAUER, M.J. and HIATT, A.J. (1966). Photoreversible control of leaf shape and chlorophyll content in *Nicotiana tabacum*. *Tob. Sci.* 10: 29-32.
- KASPERBAUER, M.J., TSO, T.C. and SOROKIN, T.P. (1970). Effect of end-of-day red and far-red radiation on free sugars, organic acids, and amino acids in tobacco. *Photochemistry* 9: 2091-2095.
- KASPERBAUER, M.J. and PEASLEE, D.E. (1973). Morphology and photosynthetic efficiency of tobacco leaves that received end-of-day red or far-red light during development. *Plant Physiol.* 52: 440-442.
- KATO, R., TADAKI, Y., and OGAWA, H. (1978). Plant biomass and growth increment studies in Pasoh forest. *Malay. Nat. J.* 30: 211-224.
- KEAY, R.W.J. (1949). *An outline of Nigerian vegetation.* Govt. Printer, Nigeria.



- KENNEDY, J.D. (1936). Forest Flora of Southern Nigeria. Government Printer, Lagos.
- KING, K.F.S. (1980). Forestry's contribution to social and community development. *Comm. For. Rev.* 59(4): 515-525.
- KTO, P.R.O. (1976). What future for natural regeneration of tropical high forest ? An appraisal with examples from Nigeria and Uganda. *Comm. For. Rev.* 55(4): 309-318.
- KNEES, G.S. and GARDNER, F.M. (1983). Mahoganies: Candidates for the Red Data Book. *Oryx*. 17: 88-92.
- KÖRNER, C. and CERNUSCA, A. (1976). A semi-automatic recording diffusion porometer and its performance under alpine field conditions. *Photosynthetica* 10: 172-181.
- KOYAMA, H. (1981). Photosynthetic rates in lowland rainforest trees of Peninsular Malaysia. *Jap. J. Eco.* 31: 361-369.
- KRAMER, J.P. and KOZLOWSKI, T.T. (1979). *Physiology of Woody Plants* Academic Press, New York, San Francisco, London.
- KRETCHMER, P.J., OZBUN, J.L., KAPLAN, S.L., LAING, D.R. and WALLACE, D.H. (1977). Red and far-red light effects on climbing in *Phaseolus vulgaris* L. *Crop Sci.* 17: 797-799.
- KVĚT, J., ONDOK, J.P., NEČAS, J. and JARVIS, P.G. (1971). Methods of growth analysis. In *Plant Photosynthetic Production : Manual of Methods*. (Eds. Z. Šesták, J. Čatský and P. G. Jarvis), pp. 343-391. Dr. W. Junk, N.V., The Hague.
- LADIPO, D.O. (1981). Branching patterns of the Tropical Hardwood *Triplochiton scleroxylon* K. schum with Special Reference to the selection of superior clones at an Early Age. Ph.D.Thesis, University of Edinburgh.
- LADIPO, D.O., GRACE, J., SANDFORD, A.P. and LEAKEY, R.R.B. (1984). Clonal variation in photosynthetic and respiration rates and diffusion resistances in the tropical hardwood *Triplochiton scleroxylon* K. schum. *Photosynthetica* 18(1): 20-27.
- LAMB, B.F. (1966). *Mahogany of Tropical America*. Ann Arbor, The University of Michigan Press.
- LAMB, A.F.A. and NTIMA, O.O. (1971). Monographs on Fast growing timber trees of the lowland tropics. No. 5. *Terminalia ivorensis*. Commonwealth Forestry Institute, Oxford.
- LANGDALE-BROWN, I., OSMASTON, H.A. and WILSON, J.G. (1964). The



- vegetation of Uganda and its bearing on land-use. Uganda Government Printer, Entebbe.
- LANGENHEIM, J.H., OSMOND, C.B., BROOKS, A. and FERRAR, P.J. (1984). Photosynthetic responses to light in seedlings of selected Amazonian and Australian rain forest tree species. *Oecologia* 63: 215-224.
- LANLY, J.P. and CLEMENT, J. (1979). Present and future natural forest and plantation areas in the tropics. *Unasylva* 31(123):12-20.
- LARCHER, W. (1969). The effect of environmental and physiological variables on the carbon dioxide gas exchange of trees. *Photosynthetica* 3(2): 167-198.
- LARCHER, W. (1980). *Physiological Plant Ecology*. Springer-Verlag, Berlin, Heidelberg, New York.
- LAWTON, R.M. (1976). State of knowledge Report on Tropical Forest Ecosystems of Anglophone Africa (copyright by UNESCO).
- LEE, R. (1978). *Forest Microclimatology*. Columbia University Press.
- LEGGATE, J.D. (1966). A summary of the performance of various species in departmental trial plots. Tech. Note 1/66. Br. Sol. Is. Prot. Forestry Dept., Honiara.
- LEOPOLD, A.C. and GUERNSEY, F.S. (1954). Respiratory responses to red and infra-red light. *Physiol. Plant.* 7: 30-40.
- LEVERENZ, J.W. (1979). Convexity and net quantum efficiency of the light response curve of photosynthesis. Swedish Coniferous Forest Project. Technical Report 25.
- LEVINGSTON, R. and ZAMORA, R. (1983). Medicine trees of the Tropics. *Unasylva* 35(140): 7-10.
- LEVITT, J. (1980). *Responses of Plants to Environmental stresses*. Volume II: Water, Radiation, Salt and other stresses. Academic Press, London, New York, Toronto, Sydney and San Francisco.
- LEWANDOWSKA, M. and JARVIS, P.G. (1977). Changes in chlorophyll and carotenoid content, specific leaf area and dry weight fraction in Sitka spruce, in response to shading and season. *New Phytol.* 79: 247-256.
- LIND, E. and VISSER, S. (1962). A study of a swamp at the North end of Lake Victoria. *J. Ecol.* 50: 599-613.
- LINDER, S. (1974). A proposal for the use of standardized methods for chlorophyll determinations in ecological and eco-physiological



- investigations. *Physiol. Plant* 32: 154-156.
- LOACH, K. (1967). Shade tolerance in tree seedlings. I. Leaf photosynthesis and respiration in plants raised under artificial shade. *New Phytol.* 66: 607-621.
- LOACH, K. (1970). Shade tolerance in tree seedlings. II. Growth analysis of plants raised under artificial shade. *New Phytol.* 69: 273-286.
- LOMMEN, P.W., SCHWINTZER, C.R., YOCUM, C.S. and GATES, D.M. (1971). A model describing photosynthesis in terms of gas and enzyme kinetics. *Planta* 98: 195-220.
- LONGMAN, K.A. and JENÍK, J. (1974). Tropical forest and its environment. Longman Inc. New York, U.K., Singapore.
- LUDELOW, M.M. and JARVIS, P.G. (1971). Photosynthesis in Sitka spruce (*Picea sitchensis* [Bong.] Carr.). 1. General characteristics. *J. Appl. Ecol.* 8: 925-953.
- LUGO, A.E. and BROWN, S. (1980). Tropical Forests: Sources or sinks of atmospheric carbon ? *Ambio.* 32(129): 8-13.
- LUGO, A.E., SCHMIDT, R. and BROWN, S. (1981). Tropical forests in the Caribbean. *Ambio.* 10(6): 318-324.
- MacGREGOR, W.D. (1934). Silviculture of the mixed deciduous forests of Nigeria. Oxford Forestry Memoirs. No. 18.
- MASAROVIČOVÁ, E. and ELIÁŠ, P. (1980). Chlorophyll content in leaves of plants in an oak-hornbeam forest. *Photosynthetica* 14(4): 604-610.
- MASAROVIČOVÁ, E. and ELIÁŠ, P. (1981). Chlorophyll content in leaves of plants in an oak-hornbeam forest. *Photosynthetica* 15(1): 16-20.
- MASKELL, E.J. (1928). Experimental researches in vegetable assimilation XVIII. Proceedings of the Royal Society, B.102: 488-533.
- MAYER, A.M. and POLJAKOFF-MAYBER, A. (1963). The germination of seeds. Pergamon Press, London.
- MILNER, C. and HUGHES, R.E. (1968). Methods of measurement of the primary production of grasslands. IBP Handbook No. 6.
- MOHMOUD, A. and GRIME, J.P. (1974). A comparison of negative relative growth rates in shaded seedlings. *New Phytol.* 73: 1215-1219.
- MIRANDA, H.S. (1982). A model of canopy photosynthesis and transpiration for Sitka spruce (*Picea sitchensis* [Bong.] Carr.). Ph.D. Thesis, University of Edinburgh.
- MORALES, D., JIMENEZ, M.S., IRIARTE, J. and GIL, F. (1982). Altitudinal effect on chlorophyll and carotenoid concentrations in gymno-



- sperms leaves. *Photosynthetica* 16(3): 362-372.
- MOONEY, H.A., BJÖRKMAN, O., HALL, A.E., MEDINA, E. and TOMLINSON, P.B. (1980). The study of the physiological ecology of tropical plants. Current status and needs. *Bio Science* 30: 22-26.
- MOONEY, H.A., FIELD, C. and VÁZQUEZ-YÁNES, C. (1984). Photosynthetic characteristics of wet tropical forest plants. In *Physiological Ecology of Plants of the Wet Tropics*. (Eds. E. Medina, H. A. Mooney and C. Vázquez-Yánes). *Tasks for vegetation sciences* 12: 113-128. Dr. W. Junk, The Hague, Boston, Lancaster.
- MORGAN, D.C. and SMITH, H. (1981a). Non photosynthetic responses to light quality. In *Encyclopedia of Plant Physiology: Physiological Plant Ecology. I. Responses to the Physical environment*. (Eds. O. L. Lange, P. S. Nobel, C.B. Osmond and H. Ziegler), New series, Vol. 12A:108-134. Springer-verlag, Berlin, Heidelberg, New York.
- MORGAN, D.C. and SMITH, H. (1981b). Control of development in *Chenopodium album* L. by shadelight: the effect of light quantity (total fluence rate) and light quality (red:far-red ratio). *New Phytol.* 88: 239-248.
- MURRAY, D.B. (1961). Shade and fertilizer relations in the banana. *Trop. Agric. Trin.* 38: 123-131.
- MURRAY, D.B. and NICHOLS, R. (1966). Light, shade and growth in some tropical plants. In: *Light as an ecological factor*. (Eds. R. Bainbridge, G. C. Evans and O. Rackham) Blackwell, Oxford pp. 249-263.
- MYRES, N. (1980). Conversion of Tropical Moist forests. Report of a survey to the U.S. National Academy of Sciences. National Resource Council, Washington D.C., April, 1980.
- MYRES, N. (1981). The Humburger connection: How Central America's forests become North America's hamburgers. *Ambio* 10(1): 3-8.
- MCCREE, K.J. (1972a). The action spectrum, absorptance and quantum yield of photosynthesis in crop plants. *Agric. Meteorol.* 9: 191-216.
- MCCREE, K.J. (1981). Photosynthetically active radiation. In *Encyclopedia of Plant Physiology* (Eds. O.L.Lange, P.S.Nobel, C.B.Osmond and H. Zeigler). *Physiological Ecology* 1. Vol.12A: 41-55. Springer-Verlag, Berlin, Heidelberg, New York.



- McCREE, K.J. and KEENER, M.E. (1974). Effect of atmospheric turbidity on the photosynthetic rates of leaves. *Agric. Meteorol.* 13: 349-357.
- McGOVERN, N.J. (1981). Bonding in papyrus-like mats from pith sections of certain plants. *TAPPI Proceedings: Pulping Conference*, pp. 35-59.
- McLAREN, J.S. and SMITH, H. (1978). Phytochrome control of growth and development of *Rumex obtusifolius* under simulated canopy light environment. *Plant Cell Environ.* 1: 61-67.
- McLEAN, R.C. (1919). Studies in the ecology of Tropical Rain forest: with special reference to the forests of South Brazil. *J. Ecol.* 7: 15-54, 121-172.
- NEWMBOULD, P.J. (1974). Methods of estimating the primary production of forests. *IBP Handbook No. 2*.
- NICHOLSON, D.I. (1960). Light requirements of seedlings five species of Dipterocarpaceae. *Malay. Forester* 23: 344-356.
- NOBEL, P.S., ZARAGOSA, L.J. and SMITH, W.K. (1975). Relationship between mesophyll surface area, photosynthetic rate, and illumination level during development of leaves of *Plectranthus parviflorus* Henekel. *Plant Physiol.* 55: 1067-1070.
- OKALI, D.U.U. (1971). Rates of dry-matter production in some tropical tree seedlings. *Ann. Bot.* 35: 87-97.
- OKALI, D.U.U. (1972). Growth-rates of some West African forest-tree seedlings in shade. *Ann. Bot.* 36: 953-959.
- OKALI, D.U.U. (1982). Africa: research to conserve the environment. *Unasylva*. 34(136): 1-8.
- ONDOK, J.P. (1971a). Calculation of mean leaf area ratio in growth analysis. *Photosynthetica* 5: 269-271.
- ONYEAGOCHA, S.C. (1962). The development of the system of natural regeneration in Malaya compared with Nigeria. Special study. *Comm. For. Inst. Oxford*. Unpubl.
- OSENI, M.A. (1980). Development of local markets for secondary species with special reference to Nigeria. *Proceedings of the Commonwealth Forestry Conference in Trinidad*.
- OSMOND, C.B., BJÖRKMAN, O. and ANDERSON, D.J. (1980). *Physiological Processes in Plant Ecology*. Springer-Verlag, Berlin, Heidelberg, New York.



- OSONUBI, O. and DAVIES, W.J. (1980). The influence of water stress on photosynthetic performance and stomatal behaviour of seedlings subjected to variation in temperature and irradiance. *Oecologia*. 46: 1-6.
- PARK, R.B. and SANE, P.V. (1971). Distribution of function and structure in chloroplast lamellae. *Ann. Rev. Plant Physiol.* 22: 395-430.
- PARKER, R.E. (1979). *Introductory Statistics for Biology*. (second edition). Studies in Biology. No. 43. Edward Arnold, London.
- PARKINSON, K.J. (1971). Carbon dioxide Infra-red gas analysis. *J. Expt. Bot.* 22(7):169-176.
- PARKINSON, K.L. and LEGG, B.J. (1972). A continuous flow porometer. *J. Appl. Ecol.* 9: 669-675.
- PEARCY, R.W. (1983). The light environment and growth of  $C_3$  and  $C_4$  tree species in the understory of a Hawaii forest. *Oecologia* 58: 19-25.
- PEARCY, R.W. and CALKIN, H.W. (1983). Carbon dioxide exchange of  $C_3$  and  $C_4$  tree species in the understory of a Hawaiian forest. *Oecologia* 58: 26-32.
- PERSSON, R. (1974). World forest resources: Review of the World's forest resources in early 1970's. Research Notes No. 17 (Department of Forest Survey, Royal College of Forestry, Stockholm).
- PHILLIPS, M.S. (1962). Working Plan for Budongo Central Forest Reserve (including Budongo, Siba and Kitigo forests). Third revision (1964-1974). Uganda Government Printer, Entebbe.
- PONS, T.L. (1977). An ecophysiological study in the field layer of ash coppice. II. Experiments with *Geum urbanum* and *Cirsium paulstre* in different light intensities. *Acta. Bot. Neerl.* 26: 29-42.
- POORE, D. (1976). The value of tropical moist forest ecosystems and the environmental consequences of their removal. *Unasylva* 28 (112-113): 127-143.
- POORE, M. E.D. and ALLARBY (1980). FAO Report on Tropical Forests.
- PRIOUL, J.L. and CHARTIER, P. (1977). Partitioning of transfer and carboxylation components of intercellular resistance to photosynthetic  $CO_2$  fixation: A critical analysis of the methods used. *Ann. Bot.* 41: 789-900.
- PROCTER, J.T.A., WATSON, R.L. and LANDSBERG, J.J. (1976). The carbon



- budget of a young apple tree. J. Amer. Soc. Hort. Sci. 101: 579-582.
- RADFORD, P.J. (1967). Growth analysis formulae their use and abuse. Crop Sci. 7: 171-175.
- RICHARDS, P.W. (1952). The Tropical Rain Forest. Cambridge University Press, London.
- ROBICHAUX, R.H. and PEARCY, R.W. (1980). Photosynthetic responses of  $C_3$  and  $C_4$  species from cool, shaded habitats in Hawaii. Oecologia 47: 106-109.
- ROBINOWITCH, F.J. (1951). Photosynthesis and Related Processes. Vol. II. Interscience, New York.
- ROSS, J. (1975). Radiative transfer in plant communities. In: Vegetation and the Atmosphere Vol. 1. Principles. (Ed. J. L. Monteith) pp. 13-55. Academic Press, London, New York, San Francisco.
- ROSS, G. J. S. (1981). The use of non-linear regression methods in crop modelling. In Mathematics and Plant Physiology (Eds. D. A. Rose and D. A. Charles-Edwards), pp. 269-282. Academic Press, London, New York, Toronto, Sydney, San Francisco.
- RUBINOFF, I. (1983). A strategy for preserving tropical rainforests. Ambio. 12(5): 255-258.
- RZÓSKA, J. (1974). The upper Nile swamps, a tropical wetland study. Freshwater Biology 4: 1-30.
- SATOH, K. (1970). Mechanism of photoinactivation in photosynthetic systems. 1. The dark reaction in photoinactivation. Plant Cell Physiol. 11: 15-27.
- SCHULZ, J.P. (1960). Ecological studies on Rain Forest in Northern Suriname. Vol. 2 of The Vegetation of Suriname. Amsterdam, North-Holland.
- SENER, M., SCHÖTZ, F. and BECK, E. (1975). Seasonal changes in structure and function of spruce chloroplasts. Planta 126: 1-10.
- ŠESTÁK, Z. (1966). Limitation for finding a linear relationship between chlorophyll content and photosynthetic activity. Biol. Plant 8: 336-346.
- ŠESTÁK, Z. (1971). Determination of chlorophylls a and b. In: Plant Photosynthetic Production : Manuals of Methods. (Eds. Z. Šesták, J. Čátský and P. G. Jarvis), pp. 672-701. Dr. W. Junk, N.V. Publishers, The Hague.



- ŠESTÁK, Z. (1977). Photosynthetic characteristics during ontogenesis of leaves. 1. Chlorophylls. *Photosynthetica* 11: 367-448.
- ŠESTÁK, Z., ČATSKÝ, J. and JARVIS, P.G. (1971). *Plant Photosynthetic Production : Manuals of Methods*. The Hague, Dr. W. Junk, N.V.
- SINCLAIR, T.C. and LEMON, E.R. (1973). The distribution of 660 and 730 nm radiation in corn canopies. *Sol. Energy*. 15: 89-97.
- SMITH, D.M. (1962). *The Practice of Silviculture*. John Wiley and Sons, Inc., New York, London.
- SMITH, H. (1973). Light quality and germination: ecological implications. In *Seed Ecology*, (Ed. W. Heydecker), pp.219-231. London, Butterworth.
- SMITH, H. (1981). Function, evolution and action of plant photoreceptors. In *Plants and the Daylight Spectrum*, Ed. H. Smith, pp. 499-508. Academic Press, London.
- SMITH, H. (1981). Light quality as an ecological factor. In *Plants and their Atmospheric Environment*, (Eds. J. Grace, E. D. Ford and P. G. Jarvis) pp. 93-110. Blackwell, Oxford.
- SMITH, H. (1981). Evidence that  $P_{fr}$  is not the active form of phytochrome in light grown maize. *Nature* 293: 163-165.
- SMITH, H. (1982). Light quality, photoreception, and plant strategy. *Ann. Rev. Plant Physiol.* 33: 481-518.
- SMITH, H. (1983). Adaptation to shade. In *Physiological processes Limiting Plant Productivity*, Ed. C. B. Johnson, pp. 159-173. Butterworth: London.
- SNEDECOR, G.W. and COCHRAN, W.G. (1967). *Statistical Methods* 6th Edn., Iowa State University Pres.
- SOKAL, R.R. and ROHLF, F.J. (1969). *Biometry*. Freeman, London.
- SOMMER, A. (1976). Attempts at an assessment of the World's tropical forests. *Unasylva*. 28(112-113): 5-25.
- SPEARS, J.S. (1979). Can the wet tropical forest survive ? *Comm. For. Rev.* 58(3): 165-180.
- SPENCE, D.H.N. (1981). Light quality and plant response under water. In *Plants and the Daylight Spectrum*. (Ed. H. Smith), pp. 245-276. Academic Press, London.
- SPENCE, D.H.N., CAMPBELL, R.M. and CHRYSTAL, J. (1971). Spectral



- intensity in some Scottish freshwater lochs. *Freshwater Biol.* 1: 321-337.
- STEENIS, C.G.G. Van (1958). Rejuvenation as a factor for judging the status of vegetation types. The biological nomad theory. In: *Proceedings of the Symposium on humid tropics vegetation*, Kandy. UNESCO, Paris. pp. 212-215.
- STEINLIN, H.J. (1982). Monitoring the World's Tropical Forests. *Unasylva*. 34(137): 2-10.
- STOUTJESDIJK, P.H. (1972). A note on the spectral transmission of light by tropical rainforest. *Acta. Bot. Neerl.* 21: 346-350.
- SYNNOTT, T.J. (1975). Factors Affecting the Regeneration and Growth of Seedlings of *Entandrophragma utile* (Dawe and Sprague) sprague. Ph.D.Thesis. Makerere University, Kampala.
- TASKER, R. (1977). Phytochrome and the radiation environment of woodlands. Ph.D.Thesis, University of Nottingham.
- TAYLORSON, R.B. and BORTHWICK, H.A. (1969). Light filtration by foliar canopies; significance for light-controlled weed seed germination. *Weed Science* 17: 48-51.
- THE NATIONAL ACADEMY OF SCIENCES (1975). Underexploited Tropical Plants with Promising Economic Value. Washington D.C.
- THOMPSON, K. (1976a). Swamp development in the headwaters of the Nile. In *The Nile: Biology of an Ancient River* (Ed. J. Rzóska). pp. 177-196. The Hague, Junk.
- THOMPSON, K. (1976b). The primary productivity of African wetlands, with particular reference to the Okavango Delta. *Proceedings symposium on the Okavanga Delta and its Future Utilization*. pp. 67-79. Botswana, Gaborone.
- THOMPSON, K., SCHEWRY, R.P. and WOOLHOUSE, W.H. (1978).. Papyrus swamp development in the Upemba Basin, Zaire : Studies of population structure in *Cyperus papyrus* stands. *Bot. J. Linn. Soc.* 78(4): 229-316.
- THORNLEY, J.H.M. (1976). Mathematical models in plant physiology. Academic Press, London.
- THORPE, M.R., SAUGIER, B., AUGER, S., BERGER, A. and METHY, M. (1978). Photosynthesis and transpiration of an isolated tree: model and validation. *Plant Cell and Environment* 1: 269-277.
- TISSEVERASINGHE, A.E.K. (1981). Timber utilization in the Tropical Lowland



- Forests. Comm. For. Rev. 60(3): 197-205.
- TRENAMAN, K.W. (1956). Working Plan for the Budongo, Siba and Kitigo Central Forest Reserves - Bunyoro District. Second revision period. 1955-1964. Forest Department, Government Printer, Uganda.
- TROUP, R.S. (1921). The silviculture of Indian trees. Vol. II. Clarendon Press, Oxford.
- TUCKER, D.J. and MANSFIELD, T.A. (1972). Effects of light quality on apical dominance of *Xanthium strumarium* and associated changes in endogenous levels of abscisic acid and cytokinins. *Planta* 102: 140-151.
- VAARTAJA, O. (1962). The relationship of fungi to survival of shaded tree seedlings. *Ecology* 43: 547-549.
- VÁZQUEZ-YÁNES, C. (1980). Light quality and seed germination in *Cecropia obtusifolia* and *Piper auritum* from a tropical rainforest in Mexico. *Phyton* 38: 33-35.
- VÁZQUEZ-YÁNES, C. and OROZCO SEGOVIA, A. (1982). Seed germination of a tropical rainforest pioneer tree (*Heliocarpus donellsmithii*) in response to diurnal fluctuations of temperature. *Physiol. Plant.* 56: 295-298.
- VÁZQUEZ-YÁNES, C. and SMITH, H. (1982). Phytochrome control of seed germination in the tropical rainforest pioneer trees (*Cecropia obtusifolia* and *Piper auritum*) and its ecological significance. *New Phytol.* 92: 477-485.
- VEZINA, P.E. and BOULTER, D.W.K. (1966). The spectral composition of near UV and visible radiation beneath forest canopies. *Can. J. Bot.* 44: 1267-1284.
- VINCE-PRUE, D. (1976). Photocontrol of petiole elongation in light-grown strawberry plants. *Planta* 131: 109-114.
- WADSWORTH, R.M. and LAWTON, J.R.S. (1968). The effect of light intensity on the growth of seedlings of some tropical tree species. *J. W. Afr. Sci. Ass.* 13: 211-214.
- WALKER, D. (1979). Energy, Plants and Man : Readers in Plant Productivity. Packard, U.K.
- WALLACE, L.I. and DUNN, E.L. (1980). Comparative photosynthesis of three gap phase successional tree species. *Oecologia* 45: 331-340.
- WATT, A.S. (1947). Pattern and process in the plant community. *J.*



- Ecol. 35: 1-22.
- WEBER, N.A. (1942). A biocoenose of papyrus heads (*Cyperus papyrus*). Ecology 23(1): 115-119.
- WHITMORE, T.C. (1965). A study of light conditions in forests in Ecuador with some suggestions for further studies in tropical forests. In: Light As An Ecological Factor. (Ed. R. Bainbridge, G.C. Evans and O. Rackham), pp. 235-247. Blackwell Scientific Publications, Oxford.
- WHITMORE, T.C. (1975). Tropical rain forests of the Far East. Clarendon Press, Oxford.
- WHITMORE, T.C. (1978). Gaps in the forest canopy. In: Tropical trees as living systems (Ed. by P. B. Tomlinson and M. H. Zimmermann), pp. 639-655. University Press, Cambridge.
- WHITMORE, T.C. (1982). On pattern and process in forests. In: The plant community as a working mechanism (Ed. E.I. Newman), pp. 45-59. Blackwell, Oxford.
- WHITMORE, T.C. and GONG WOOI-KHOON (1983). Growth analysis of the seedlings of Balsa, *Ochroma lagopus*. New Phytol. 95: 305-311.
- WHITMORE, T.C. and WONG, Y.K. (1959). Patterns of sunlight and shade in tropical rain forest. Malay. Forester 21: 50-62.
- WIESNER, J. (1895). Untersuchungen über den Lichtgenuss der Pflanzen mit Rücksicht auf die vegetation von Wein, Kairo und Buitenzorg (Java). S.B.Akad.Wiss.Wien, Math. Naturw. Cl., 104: 605-711.
- WIESNER, J. (1907). Der Lichtgenuss der Pflanzen. Leipzig.
- WILLAN, R.L. (1966). Natural regeneration of high forest in Tanganyika. E. Afr. Agric. For. J. 31: 43-53.
- WILLIAMS, R.F. (1946). The physiology of plant growth with special reference to the concept of net assimilation rate. Ann. Bot. 10: 41-72.
- WILLMOT, A. and MOORE, P.D. (1973). Adaptation to light intensity in *Silene alba* and *S. dioica*. Oikos. 24: 458-464.
- de WIT, C.T. (1965). Photosynthesis of leaf canopies. Agricultural Research Report No. 663. Centre for Agricultural Publications and Documentation, Wageningen 1-57.
- WOODWARD, F.I. (1981). Shoot extension and water relations of *Circaea lutetiana* in sunflecks. In Plants and their Atmospheric Environment. (Ed. J. Grace, E. D. Ford and P. G. Jarvis) pp.



- 83-91. Blackwell Scientific Publications, Oxford, London, Edinburgh, Boston, Melbourne.
- WOODWELL, G.M., WHITTAKER, R.H., REINERS, W.A., DELWICHE, C.C. and BOTKIN, D.B. (1978). The Biota and the World Carbon Budget. *Science*. 199(4325): 141-145.
- WOOLFEY, J.T. (1971). Reflectance and transmittance of light by leaves. *Plant Physiol.* 47: 656-662.
- WORLD BANK REPORT (1978). Sector Policy Paper - Forestry. World Bank, Washington, D.C.
- YOCUM, C.S., ALLEN, L.H. and LEMON, E.R. (1964). Photosynthesis under field conditions: VI. Solar radiation balance and photosynthesis efficiency. *Agron. J.* 56: 249-253.
- ZEIGLER, R. and EGLER, K. (1965). Zur quantitativen Analyse der chloroplastenpigmente. 1. Kritische überprüfung der Spektralphotometrischen chlorophyll-Bestimmung. *Beitr. Biol. Pflanzen* 41: 11-37.